SPAWNING PATTERNS AND RETENTION AND DISPERSAL OF EARLY LIFE STAGES OF ATLANTIC COD (Gadus morhua) IN A NEWFOUNDLAND FJORD

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Spawning patterns and retention and dispersal of early life stages of Atlantic cod (*Gadus morhua*) in a Newfoundland fjord

By

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Abstract

Ichthyoplankton and hydroacoustic surveys were used to examine Atlantic cod (*Gadus morhua*) distribution and behaviour as well as cod egg abundance and distribution during spring and summer 2006 and 2007 to infer on cod spawning activity in Smith Sound, a known overwintering area on Newfoundland's northeast coast. In the first section of the thesis, estimated spawning times from egg abundance and distribution patterns and environmental data suggested a prolonged spawning period with spring and summer spawning peaks. Spring egg distribution indicated dispersal of eggs out of the Sound. In summer, egg and larval densities were highest within the innermost portion of the Sound, suggesting significant retention and local development. In the second part of the thesis, acoustic measurements of cod behaviour were closely linked with egg production times adding further support that vertical shoaling behaviour is associated with reproduction of cod in the wild.

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Introduction

The Atlantic cod (*Gadus morhua*) is a temperate species found throughout the Northwest and Northeast Atlantic (Rose 2007). Cod are primarily demersal but can be found at mid-water and near the surface. They inhabit a range of marine habitats from shallow coastal waters to the edge of the continental shelf (Scott and Scott 1988). Distinct inshore and offshore stocks exist, however the delineation of sub-populations is not always clear and geographic distributions invariably overlap, particularly as cod undergo seasonal migrations (Brander 2005). Historically, cod was the most important fish species in the Northwest Atlantic, supporting a fishery for centuries. Newfoundland's 'northern cod' stock (NAFO subdivisions 2J and 3KL) was the most abundant - reaching a historical maximum of 3.5 million tonnes (Rose 2007). After a dramatic decline during the 1980's and early 1990's, fishing bans were imposed on all stocks. To date, most offshore stocks remain at very low levels (DFO CSAS Report 2008/034) and the directed fishery for northern cod remains closed.

Despite the known existence of inshore stock components of cod in major bays and inlets along the Newfoundland and Labrador coastline, only recently have these populations gained interest from research scientists (Wroblewski *et al.* 2005). Since the collapse of northern cod, research interest has shifted to understanding the importance of the major inshore stocks for rebuilding the fishery. It has been hypothesized that many bays and inlets around Newfoundland constitute prime cod habitat and that out-migration from these areas may help restore the offshore stocks (Wroblewski *et al.* 2005; Rose *et al.* 2008). Hence, understanding the spawning patterns of these coastal groups and the

potential fate of offspring produced is an important step in establishing recovery strategies for Newfoundland's cod stocks.

Indirect evidence of inshore spawning in Newfoundland waters was described by Hutchings *et al.* (1993), who reported cod in spawning condition dispersed over the continental shelf and inshore areas. Smedbol and Wroblewski (1997) provided the first direct evidence of inshore spawning in Newfoundland waters using a multi-method approach. Spawning patterns of cod in Placentia Bay, Newfoundland, were also described by Lawson and Rose (2000a). Despite these studies, gaps remain in our understanding of the timing and location of spawning by cod in inshore areas of Newfoundland. This is partly due to the reproductive biology of cod which spawn over a protracted period and the limitations of using individual methods to identify spawning cod: acoustic methods allow vast areas of the sea to be surveyed but are limited by near-ground detectability (Lawson and Rose 1999). Egg and larval surveys in conjunction with temperature dependent development models can provide estimates of spawning times and locations (e.g., Brander and Hurley 1992) but are restricted by assumptions and uncertainties about drift patterns (Pepin and Helbig 1997). Furthermore, analysis of maturity stage from trawl catch data and/or research trawls may be influenced by low spatial resolution or variability in fishing effort and fish distribution (especially if aggregations are distributed semi-pelagically) (Hutchings *et al.* 1993).

Atlantic cod employ a reproductive strategy whereby a large amount of energy is allocated to the development of high numbers (a few hundred thousand to many million) of eggs of which only a very small fraction survives to maturity. Fecundity and female size are directly related (e.g. Fudge and Rose 2008a). Cod are determinate (fecundity is

determined prior to the onset of spawning), broadcast spawners that release multiple batches of eggs at intervals over an extended spawning period (Scott and Scott 1988). Spawning occurs annually although it has been suggested that skipped spawning could occur for individuals in some stocks (Rideout *et al.* 2005). Cod form sex-segregated groups on or near the spawning grounds, with males arriving first (Morgan and Trippel 1996; Robichaud and Rose 2002; Windle and Rose 2007). Captive studies have shown that reproduction in Atlantic cod involves a range of behaviours within and between sexes (Brawn 1961; Hutchings *et al.* 1999). Males aggressively establish and defend "territories" (i.e., small (~4-7 m^3) volumes of water) during the pre-spawning period, that are either horizontally (Brawn 1961) or vertically (Hutchings *et al.* 1999) separated from the main group of females, resulting in the formation of dominance hierarchies that are believed to influence reproductive access to females (Brawn 1961; Hutchings *et al.* 1999). These studies have also shown that highly structured courtship behaviours between the sexes occur at the time of spawning. Females initiate spawning by entering a male territory, at which time the male performs an array of courtship behaviours that include flaunting, circling, and vocalizations produced by drumming muscles surrounding the swim bladder (Brawn 1961; Hutchings *et al.* 1999; Nordeide and Kjellsby 1999). Eggs are fertilized externally during a ventral mount by the male and are buoyant or semi-buoyant depending on the physical properties of the ambient water. Development rates are dictated largely by water temperature (Pepin *et al.* 1997). Developing eggs and larvae drift with the surrounding environment. No parental care is provided to offspring.

Spawning 'columns' (i.e., vertical aggregations of spawning cod) were first described by Rose (1993) who observed them in migrating cod on the northeastern

Newfoundland shelf. According to Rose, columns may have comprised pairs or small groups of cod engaged in pelagic pre-spawning courtship. Since then, observations of spawning columns have been reported by many others (Ouellet *et al.* 1997; Lawson and Rose 2000a; Fudge and Rose unpublished data). Although it still remains unclear whether the release of eggs and milt is actually occurring during the formation of these aggregations, their presence at predicted spawning times and locations in different geographic regions has added further weight to the theory that they are associated with cod reproduction.

In cod and other marine fishes that produce pelagic eggs, successful survival during early life stages typically depends on retention in, or transport to, environments favourable for growth and survival (Jennings *et al.* 2001). Therefore, the synchronicity of spawning and the physical processes that promote retention or transportation has a significant impact on egg and larval survival and hence, recruitment. Indeed, variation in spawning times, temperature and physical processes (i.e., winds, tides and currents) and production cycles accounts for most of the annual variation in recruitment in many species (Page and Frank 1989; deYoung and Rose 1993). It has been theorized that the coincidence of reproduction and favourable environmental conditions based on high food availability (Cushing 1969; 1990), low predation (Frank and Leggett 1982; Leggett 1985; Pepin *et al.* 1995), or transport to nursery areas (Harden Jones 1968; Sinclair 1998) has led to the evolution of specific spatial and temporal spawning patterns.

Historically, fisheries managers have relied on stock abundance estimates from trawl and acoustic surveys, general distribution patterns of target species, and information on stock structure based on commercial catch records to guide management decisions

(Hutchings 2000). Fish behaviour was typically discounted as important to assessments of stock status and therefore management. Just as improvements to existing fisheries assessment techniques from the development of statistical models, more precise measurement tools and technological advancements have increased the ability of fisheries scientists and managers to provide sustainable management, the collapse of some fisheries and the steady decline of many others (Taggart *et al.* 1994; Hutchings and Reynolds 2004) has brought on an appeal for new and better approaches to traditional fisheries management strategies (e.g., Hutchings 2000). Many proponents claim that implementing knowledge of ecological and behavioural traits of commercially important marine fish is essential to developing better management practices (Freon *et al.* 1993; Frank and Leggett 1994; Perry and Smith 1994; Bradbury *et al.* 2000). For example, awareness of how individual and group behaviour influences catch rates has become increasingly important in management practices. Rowe and Hutchings (2003) suggested that disruption of essential behaviours associated with reproduction in cod by commercial fishing practices may result in lower spawning success and overall recruitment. It has been proposed that harvesting cod during spawning may detrimentally remove large numbers of one sex due to spatial segregation of males and females during the pre- and post-spawning period (Hutchings *et al.* 1999). Rose *et al.* (2008) also suggested that fishing on spawning aggregations may remove the largest and most fecund fish (due to the fact that fishing practices tend to target the largest, and hence, most economically valuable fish), resulting in a significant reduction in reproductive potential.

In addition to stock size estimates, acoustic methods can provide quantitative information on distribution and behaviour of many marine species (Rose 1993; Morgan *et*

al. 1997; Lawson and Rose 2000a). For example, diurnal vertical migrations of redfish (*Sebastes mentella*) were described by Gauthier and Rose (2002). Acoustics also provides high-resolution data images of the shape and size of fish shoals (Reid and Simmonds 1993; Misund *et al.* 1995; Fudge and Rose unpublished data), and therefore may be a valuable tool for describing cod formations during spawning.

In this thesis, I aimed to further our knowledge of coastal Atlantic cod by examining the spatial and temporal dynamics of spawning cod and their eggs over two spawning seasons in a coastal inlet on Newfoundland's northeast coast. A second goal of this thesis was to demonstrate that reproductively related behaviour of cod in the wild can be observed and quantified using acoustic methods.

Thesis Overview

This thesis provides knowledge of the timing and location of cod spawning in a coastal fjord in Newfoundland using hydroacoustic and ichthyoplankton methods. In chapter 1, I use ichthyoplankton surveys performed throughout the spawning season to describe the spatial and temporal patterns of cod egg abundance and to provide knowledge on the timing and location of cod spawning in a coastal fjord. The development and retention of eggs and larvae within the fjord with respect to environmental conditions is discussed. The hypotheses that (1) egg densities peak in spring and early summer and are related to adult distribution and biomass measures (as per sequential acoustic surveys) and (2) development and retention of eggs and larvae within the sound depends on wind stress and water circulation patterns and temperatures are explored. In Chapter 2, the relationship between acoustically detected behaviour patterns and spawning activity of cod using peaks in egg abundance is examined to test the hypothesis that spawning columns are associated with spawning events, as indicated by resultant egg densities and distribution.

Co-authorship Statement

I am the principal author of both research papers presented in this thesis. I was responsible for the design and implementation of the field research, as well as data analysis and manuscript preparation. Dr. George Rose is second author on both papers, and provided conceptual suggestions and aid during all stages of the thesis, including editorial comments on previous drafts.

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Chapter 1 (Knickle and Rose) will be submitted to *Marine Ecology Progress Series* or a similar journal.

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Chapter 1. Spawning timing and differential retention and dispersal of early life stage Atlantic cod (*Gadus morhua*) in a Newfoundland fjord.

1.1 Abstract

Sequential ichthyoplankton surveys were used to determine the spatial and temporal distribution of eggs and larvae over coastal spawning grounds of Atlantic cod (*Gadus morhua*) in Smith Sound, Trinity Bay, Newfoundland during the springs and summers of 2006 and 2007. Egg densities showed similar patterns for both years with peaks in abundance in spring (Mar-Apr) and late summer (late Jul). A clear progression of development stages (I-IV) was observed in spring and summer in 2006 and summer in 2007 suggesting retention of eggs within the Sound during these periods. Spatially, eggs were distributed near the surface over the length of the Sound during spring, and below the pycnocline (>10m) at the inner portions of the fjord during the summer months. Backcalculated peaks in spawning based on water temperatures were estimated at 11 and 4 April for 2006 and 2007, respectfully. Late season peaks in spawning were estimated at 21-24 July for both years. Environmental data indicated cooler water temperatures and periods of high wind stress in spring (Mar-Apr), and warmer, calmer periods late summer (Jul-Aug). It is suggested that the timing of spawning for cod, as well as environmental conditions, play an important role in the fate of propagules with higher retention and faster development times on the spawning grounds occurring later in the season. The hypothesis that differences in preferred spawning times represent separate reproductive strategies for resident and migrant fish groups is discussed.

1.2 Introduction

A conventional theory in the behavioural ecology of marine fishes states that reproductive strategies have evolved so that offspring hatch and develop at times and in areas favourable for growth and survival (e.g., Cushing 1990). For species with a pelagic ontogenetic stage, spawning in sheltered coastal areas such as in fjords, retention of eggs and larvae may be an important factor for individual reproductive success which in turn, may influence survivorship and self-maintenance of the population. For example, coastal spawning and high retention of eggs and larvae is believed to contribute to the genetic structure of coastal cod in neighbouring fjords along the Norwegian coast (Knutsen *et al.* 2007). Conversely, dispersal of eggs and larvae from inshore spawning grounds may help to ensure individual reproductive success against density-dependent mechanisms such as increased food competition and predation or may result in increased survival due to unpredictable environmental perturbations (Economou 1991). Lastly, coastal spawning may promote local recruitment and population growth and lead to density-dependent out-migration to other coastal and offshore areas (Wroblewski *et al.* 2005)

The importance of coastal embayments to various life stages of marine fishes in Newfoundland is well known (e.g. Frank and Leggett 1982, Laprise and Pepin 1995, Bradbury *et al.* 2008). For Atlantic cod, coastal environments are thought to be critical to the survival and development of early life history stages (Templeman and Fleming 1965; Anderson and Dalley 1997; Bradbury *et al.* 2000) and contain key spawning sites (Hutchings *et al.* 1993; Rose *et al.* 2008). With the exception of the latter study however,

details of the timing and location of cod spawning in coastal areas of Newfoundland remain poorly known.

Several methods have been used to estimate spawning times for Atlantic cod: otolith microstructure (Pinsent and Methven 1997), egg and larval distributions and circulation patterns (Pepin and Helbig 1997; Bradbury *et al.* 2000), gonadal condition of adults, either solely (e.g. Hutchings *et al.* 1993), or linked with hydroacoustic descriptors (Ouellet *et al.* 1997; Lawson and Rose 2000a). Egg and larval surveys provide an effective means of estimating spawning times because eggs can be aged on a relatively short time scale in comparison to other life history stages. Sequential sampling over broad temporal scales allows depiction of seasonal and interannual patterns as opposed to short term or intermittent sampling.

In 1995, three years after a moratorium was imposed on the northern cod fishery, a large aggregation of spawning cod was unexpectedly located in Smith Sound, a coastal inlet of Trinity Bay on the northeast coast of Newfoundland. This aggregation has been monitored since and has been the largest known surviving component of the once abundant northern cod stock (Rose 2003). In a typical year, cod overwinter in the deep waters of the Sound and begin to spawn in spring. A large proportion move north to Bonavista Bay by June (Brattey and Healey 2007), returning to the Sound in the fall but some fish are present within the Sound year-round (Rose 2003; 2007). Although adult spawning within the Sound has been observed for many years (Rose 2003; 2007), and elevated egg densities were found during a single sample collected during 1995 surveys (Smedbol *et al.* 1998), little information existed on the extent or timing of spawnings, or on the fate of the propagules produced.

I hypothesized that spawning would peak in spring and early summer and that the timing of spawning and environmental conditions within the Sound would influence recruitment in two ways: through advection of eggs and larvae away from the spawning site and retention and development within the Sound. The purpose of this study was to describe the spatial and temporal patterns of spawning cod and their eggs in Smith Sound using sequential ichthyoplankton surveys. Specific objectives were to: (1) quantify spatial and temporal distribution of eggs and larvae; (2) estimate timing and location of spawning from egg distribution patterns; and (3) examine retention and development of eggs and larvae within the Sound.

1.3 Methods

1.3.1 Study Area

Smith Sound is a narrow (ca. 2 km wide), zigzag shaped inlet of approximately 22 km in length situated in the western side of Trinity Bay on Newfoundland's northeast coast (Figure 1.1). Basins within the mid-line trench range from 200 to 350 m in depth with sills ranging from 150 m in the middle and outer Sound to less than 40 m at the innermost portion. Near surface water salinity is highest in early spring and lowest in early fall (E.B. Colbourne, Science Branch, DFO Newfoundland & Labrador, pers comm). Circulation patterns are not well understood, however, it is likely that surface currents are influenced largely by wind forcing, with surface and mid-water layers flowing in opposing directions depending on wind conditions (Zedel and Cyr-Racine

2008; L. Zedel Dept of Physics and Oceanography, Memorial University of Newfoundland, pers comm).

From 16 March to 6 September 2006 and 26 March to 30 August 2007, ichthyoplankton surveys were performed concurrently with hydroacoustic surveys during daylight hours (9-12 hrs to complete). Surveys were done approximately every 3 days during the spring in 2006 in an effort to obtain high resolution data on egg abundance and distribution at the onset of spawning, with less frequent surveys in summer. Preliminary results from 2006 indicated a much more protracted spawning period than originally anticipated, with multiple spawning peaks, and as a result, surveys were more evenly distributed during 2007. Ice conditions in the Sound prevented sampling during a two-week period in April of 2007.

1.3.2 Egg Collection and Analysis

Ichthyoplankton sampling was performed at 10 fixed stations (depths 35-280 m) along the axis of the Sound approximately 3-4 km apart and adjacent to the acoustic transects (Figure 1.1) using a 1-m ring plankton net (Sea-Gear Model 9000) with a 330-µm mesh size. A mechanical flowmeter (Sea-Gear Model 2030) and depth and temperature logger (Vemco Minilog data logger) were positioned at the net opening to estimate flow volume and record sampling depth and temperature profiles. Vertical-oblique tows were made at each station by lowering the net below the thermocline (<40 m) and retrieving it at a rate of ~0.5 m/s. Although tow depths varied, all sampled the upper-mixed layer of the water column where most cod eggs are concentrated (e.g.

Anderson and deYoung 1995). Tows generally took 8-10 minutes to complete. All contents were preserved on board using a 5% buffered formalin solution.

Samples were sorted in the lab and cod eggs and larvae identified and enumerated by diameter size (~1-1.5 mm). Early stage (1-3) cod eggs cannot be differentiated from those of witch flounder (*Glyptocephalus cynoglossus*) and haddock (*Melanogrammus aeglefinus*) and hence are typically classified as "Cod-Haddock-Witch" or "CHW" (Markle and Frost 1985). Witch flounder stocks in Trinity Bay (NAFO sub-division 3La) remain at very low levels (Maddock Parsons 2007) and haddock are rarely encountered in this area (DFO CSAS Report 2005/051). Furthermore, no late stage witch flounder or haddock eggs or larvae were observed during the course of the study and therefore all enumerated eggs of the specified size were assumed to be cod. Eggs were divided into one of four stages of development according to the criteria set out by Markle and Frost (1985). Stage I was from fertilization until the visible formation of an embryonic axis about the midgastrula. Stage II was from the formation of the embryonic axis until the embryo is halfway around the yolk, approximately the time of blastopore closure. Stage III was from the end of stage II until the tip of the tail reaches the snout. Stage IV was from the end of stage 3 until hatching. All eggs and larvae were photographed and measured using a digital stereomicroscope (Leica Microsystems Leica EZ4). Densities (individuals·m^{-3}) were calculated using egg and larval counts and flowmeter readings converted to volumetric measurements.

Spawning dates were back-calculated using date of peak abundance of eggs and mean temperature of the upper water column (≤40 m) applied to generalized (Page and

Frank 1989) and stock-specific (Pepin *et al.* 1997) temperature-dependent development relationships.

Egg densities were interpolated from station points using linear kriging with ArcGIS geostatistical software. The total number of eggs in the Sound was estimated by extrapolating kriged stage I egg densities to the total survey area, assuming eggs were dispersed over the entire Sound. From the spawning site, Atlantic cod eggs have the potential to be dispersed over several hundred kilometres (Bradbury et al. 2000; van der Molen et al. 2007) and were found to be dispersed over a mean distance of 25 km in a coastal embayment on Newfoundland's southern shore (Bradbury et al. 2000). It is therefore reasonable to assume that eggs spawned and collected within Smith Sound in the present study would disperse at least 2.5 km (the maximum distance from station points to shoreline), and be located throughout the study area. Egg potential (a proxy for total number of eggs produced) was calculated using a fecundity model from Fudge and Rose (2008b) and geostatistically determined acoustic numbers of cod during the study period based on methods modified from Rose (2003). A 1:1 sex ratio, assumed in estimating total number of mature females for each survey, and the percent of spawning females in each survey was determined from historical and current catch data (Knickle and Rose unpublished data).

Steady state (equilibrium between buoyancy and vertical turbulent forces) vertical distribution of eggs was predicted for spring and late summer for 2007 using density profiles of the water column applied to models developed for pelagic cod eggs from the northeastern Newfoundland shelf (Anderson and deYoung 1995) and bathypelagic eggs in the mixed layer (Sundby 1991). A constant vertical diffusivity of 1.0 $cm^2 \cdot s^{-1}$ was used

for both models (Anderson and deYoung 1995). A mean density of 1.0255 $g \cdot m^{-3}$ for field captured cod eggs was used based on studies on egg buoyancy from the Newfoundland shelf (Anderson and deYoung 1994) and northeast Gulf of St. Lawrence (Ouellet 1997).

1.3.3 Environmental Data

Temperature and salinity (2007 only) profiles were performed monthly at 3 fixed locations (Figure 1.1) using a SBE 25 SEALOGGER CTD. Continuous weather conditions were recorded from a Rainwise Inc MK-III weather station located on shore near the middle of the Sound. Daily mean wind speed and direction were calculated for the study period and wind speeds converted to wind stress using methods from Large and Pond (1981).

1.4 Results

1.4.1 Egg abundance

Egg densities showed similar temporal patterns in 2006 and 2007 with moderate peaks in April, lower concentrations in May and June and high peaks in late July (Table 1.1, Figure 1.2). Fewer eggs were observed in April of 2007 than during the previous year in conjunction with a gap in sampling (14-26 Apr) as a result of ice build-up in the Sound. Overall egg density (all stations, all stages) and density for each stage of development varied among months but not between years (Table 1.2), except for stage IV eggs which showed a statistically significant difference between years as well as months. Stage I egg

densities peaked in mid-April and late July. Stage II eggs showed similar trends but appeared and peaked, on average, a week later than stage I eggs except in April of 2007 when no peak in stage II eggs was detected, possibly due to gap in sampling. Late stage eggs (III-IV) showed the same general trend with a 2-4 week temporal shift in initial appearance and peak abundance except for in 2007 when a late-season peak in stage IV eggs may have occurred in the fall after sampling had ended. This is based on the assumption that development of abundance of stage III eggs observed (see Figure 1.2) would continue beyond sampling dates. Recently hatched yolk-sac larvae were taken throughout the field season in 2006 but were most abundant in April and May. Only two yolk-sac larvae were collected in 2007, one in April and one in August, compared to 35 in 2006.

Based on observed egg densities extrapolated to the survey area, the total number of eggs within the Sound peaked in late summer, exceeding 3.5 billion in both years (Figure 1.3). In constrast, modelled later egg potential was highest in the spring and relatively low in the summer.

1.4.2 Egg distribution

Stage I densities were highest at the innermost part of the Sound in July and August and corresponded with peak egg abundance in both years (Figure 1.4). Stage I densities varied significantly among stations in April 2006 (ANOVA, n=90, F 3.7, p=0.001) when high numbers of stage I eggs were taken at the inner-middle portion of the Sound. High numbers of stage I eggs were also collected from the inner-middle and outer Sound (station 10) during April 2007, though differences in densities among stations were

not significant. Stage I eggs were more evenly distributed among stations (showed no statistical variation) in May and early June for both years. Stage I egg densities differed significantly among stations in late June (ANOVA, $F=3.08$, $p=0.010$), July ($F=6.21$, $p<0.001$) and August ($F=4.54$, $p<0.001$) for 2007. Stage II-III eggs showed highest densities at the inner Sound later in the season (Figures 1.5 and 1.6). Stage II egg densities were significant different among stations in July 2007 ($F=3.48$, $p=0.003$). Stage III densities differed in July-September 2006 ($F= 3.00$, $p=0.019$) and July 2007 ($F= 5.90$, $p>0.001$). Stage IV eggs were more widely dispersed than earlier stages and were most commonly found at middle and inner stations (Figure 1.7). Recently hatched yolk-sac larvae were taken at various stations in 2006 but occurred mostly at the inner- and outermost stations (Figure 1.8). Overall egg densities (all stages combined) did not differ significantly among stations within months for either year.

Vertical egg distribution patterns differed seasonally and between areas in the Sound for 2007 (no data for 2006). In general, eggs were positively buoyant at the surface in the spring and negatively buoyant to about 10 m later in the summer (Figure 1.9). Eggs were concentrated at slightly greater depths in the inner Sound compared to outer stations (Figure 1.9).

1.4.3 Time of Spawning

Back-calculation of spring spawning times from peak stage I egg densities using relationships from Pepin *et al.* (1997) were estimated as 11 April in 2006 and 4 April for 2007 (Figure 1.10a). Spawning dates estimated with Page and Frank's (1989) power curve relationship between stage duration and temperature were earlier at 9 April in 2006

and 21-23 March in 2007 (Figure 1.10b). Both methods estimated major peaks in spawning activity at 21-24 July for 2006 and 2007. Moderate spawning was apparent from the presence of early stage eggs throughout May and June in both years.

A clear progression of development stages was evident from major stage I peaks particularly in April-May of 2006 when frequent sampling was conducted (Figure 1.11). Based on the proportion of stage I eggs in each sample, spawning peaked in mid to late March and in late June and late July in 2006. In 2007, the highest proportion of stage I eggs was observed at the beginning of April with increases in mid-June and late July, suggesting an increased of rate of spawning in mid to late March, early June and late July.

1.4.4 Environmental conditions for egg retention

Surface and mixed layer water temperatures in Smith Sound were generally cooler in 2007 than 2006, particularly from March through May (Figure 1.12). Mean water temperatures in 2006 increased from April to August but underwent large fluctuations in late-May and June. In contrast, 2007 water temperatures increased more gradually throughout the spring and summer, although a sharp drop in temperature (~ 4°C) throughout the study area was observed on June 25, 2007. The water column was only weakly stratified during the spring in 2007 compared to 2006 when warming of the upper 30-40 m was apparent by mid-April (Figure 1.13). Temperature profiles for each year showed similar patterns later in the season. Near surface and upper mixed layer water temperatures decreased from inner to outer stations for both years (Figure 1.13).

Water column density profiles from 2007 showed the Sound was weakly stratified with no pycnocline in the upper 150 m in late March; clear density stratification was

evident by mid-summer (Figure 1.13). Surface water density was lowest at the innermost stations, likely as a result of shallower depths and freshwater input (Figure 1.13).

South-westerly winds were predominant during the study period. Wind stress differed significantly among months for both 2006 (ANOVA, n 243, F 2.64, $p<0.05$) and 2007 ($n=251$, $F=5.15$, $p<0.05$) and showed a decrease from January to August in both years (Figure 1.14). Periods of high wind stress (indicative of storm events) were most common from late-January to May and were usually accompanied by a shift in wind direction from the East. In each year, wind stress was lowest with the fewest storm events in July and August.

1.5 Discussion

1.5.1 Spawning period

The presence of newly fertilized (stage 1) cod eggs in Smith Sound throughout the study period indicates spawning from at least March through August (larvae collected in mid April 2006 suggests spawning early as 4-21 February). These findings confirm previous but limited observations of coastal spawning in Newfoundland. For example, Pinsent and Methven (1997) concluded that newly settled larvae in Trinity Bay must have been spawned from mid-January to mid-October, but did not identify a likely source. Stage 1 cod eggs have been collected near known spawning grounds in Placentia Bay from April to August (Rose *et al.* 2008). In other regions, protracted spawning has also been shown. In the eastern Baltic Sea cod spawning begins in March and ends in August

(Brander 1994). Early studies in the coastal areas of the southern Gulf of St. Lawrence suggested spawning occurred from May to September (Powles 1958). Late season peaks in egg abundance observed in the present study are also consistent with previous reports of 'late' egg production in coastal areas of Newfoundland. Early accounts from Thompson (1943) suggested 'shore cod' in Trinity Bay spawned as late as August and September. Smedbol *et al.* (1998) found the highest egg concentrations in July and August at inner stations in a neighbouring fjord in Trinity Bay, and estimated peak spawning in the area between mid-June and mid-July. Lawson and Rose (2000a) found female cod in spawning condition as late as November in Placentia Bay. These studies together with results from the current study confirm a very protracted spawning period for cod in which late-season spawning may be more prominent than originally thought.

In comparison with offshore spawning groups in eastern Newfoundland (NAFO Division 3KL) in which a spawning period from March-early June has been suggested (Templeman 1981; Hutchings and Myers 1994), spawning in coastal groups may be more protracted (Bradbury *et al.* 2000; Lawson and Rose 2000a). It is also possible that previous results from offshore groups were limited by lack of sampling in June and July. Studies on spawning offshore cod in the early 1990's indicated intense spawning at least as late as mid-June in northern cod (Rose 1993).

The current study identified two major spawning peaks within Smith Sound that were consistent in magnitude and timing in 2006 and 2007. Female cod have been observed to release as many as 20 batches of eggs over a maximum 60 day period in laboratory studies (Kjesbu 1989). It is therefore likely that cod that spawned in April in Smith Sound finished spawning prior to the summer months and did not contribute to the

late season peaks in egg density. Timing of reproduction in cod is closely tied to water temperature during vitellogenesis and the condition of the spawning fish (Kjesbu 1994). Why then would we see such variation in the timing of reproduction? There are several plausible hypotheses. One is that peaks in spawning represent genetic or geographically distinct groups of fish. These could both overwinter in Smith Sound or be migrants. The existence of resident and migratory cod in Smith Sound (Rose 2007) and fjords in other geographic locations (Svedäng *et al.* 2007) leads to the prospect that different ecotypes could be utilizing favourable spawning grounds at different times. It is known through tagging studies that many large (>65 cm) fish migrate out of the Sound in early summer (Brattey and Healey 2007). However, cod have been observed with echosounders during the summer months for many years (Rose 2003) and cod are routinely taken during the recreational fishery in late summer. It is plausible that a migrant stock component spawns early in the year prior to undertaking coastal migration and resident cod spawn later during the summer months. Alternatively, tagging studies have shown that cod from southern offshore and coastal stocks (NAFO subdivision 3Ps and Placentia Bay) do migrate north during the summer as far as Trinity Bay (Brattey *et al.* 1999; Lawson and Rose 2000b), although most are thought to spawn prior to migration. Offshore cod from the Bonavista Corridor migrate to Trinity Bay while spawning (Rose 1993), but their numbers are so reduced as to make such an origin unlikely during the present study. Methven and Pinsent (1997) concluded that juvenile cod collected in Trinity Bay in September may have been advected from offshore spawning grounds, however, this cannot explain the high numbers of early stage cod eggs (< 3 d old) collected in late July in this study. Numerous studies have shown that size-segregated spawning occurs in

various cod stocks, including coastal Newfoundland (Lawson and Rose 2000a), Grand Banks (Hutching and Myers 1993), Gulf of St. Lawrence (Ouellet *et al.* 1997), Icelandic (Marteinsdottir and Petursdottir 1999), Baltic (Bleil and Oeberst 1997) and Norwegian (Bergstad *et al.* 1987). Although it is unresolved whether older, larger fish spawn earlier (e.g. Lawson and Rose 2000a) or later (e.g. Hutchings and Myers 1993), or both, age-specific spawning times could partly explain a prolonged spawning period of cod in Smith Sound. In conclusion, the present work indicates that the most likely source of eggs found in the Sound are from either resident or migrant cod present in the Sound.

1.5.2 Egg Distribution

The present study revealed a high level of retention within the study area and a build up of eggs at the innermost portion of the Sound, especially during July and August. Eggs of all stages were most abundant in late summer despite a lower female abundance and potential egg production (Figure 1.3), adding further evidence of higher retention rates later in the season. In particular, stage II and III egg densities were highest in July and September in 2006 and July and August in 2007.

Limits to survey coverage later in the season when adult cod are distributed in shallower waters closer to shore likely resulted in a negative bias in abundance potential. Based on low egg production potential beyond June (see figure 1.3), it would have taken approximately 20 days to accumulate the number of eggs observed. Egg development time would have been relatively short during this period (~6 days to exit stage I), hence it is probable that late season acoustic surveys were not measuring the total amount of summer spawners. However, these results (high egg abundance, lower numbers of cod)

can also be explained in part by retention mechanisms whereby wind-driven circulation dispersed eggs outside the Sound in spring and retained them in summer. In this manner, the observed increase in egg densities later in the season would be a reflection of increased retention rates and not egg production. The general circulation pattern in fjords is an outward flux of surface water and inward movement of sub-surface layers (Svendsen and Thompson 1978; Klinck *et al.* 1981; Farmer and Freeland 1983), however, this pattern is influenced by the wind and can be reversed by shifts in wind direction (Svendsen and Thompson 1978; L Zedel, Dept of Physics and Oceanography, Memorial University of Newfoundland, pers comm). The predominant south-westerly winds present in the study area during the course of the study, therefore, would have carried passive particles located in the upper surface layer out of the Sound while conveying sub-surface layers inward. Based on results of modelled vertical egg distribution (Figure 1.9) cod eggs were concentrated within the inner-moving sub-surface layer in late summer and would have been transported to the inner portions of the Sound. Conversely, with little thermal and pycnal stratification of the upper water column in spring, a higher concentration of eggs were found in the outward moving surface layer and hence, would have been advected out of the Sound (Figure 1.9). This theory of dispersal and retention of cod eggs in fjords is not new and has been used to explain similar results in studies from coastal Norway (Knutsen *et al.* 2007; Stenevik *et al.* 2008). A detailed investigation of the physical processes governing circulation patterns in Smith Sound and their role in the distribution of early life history stages of cod is beyond the scope the present paper but could provide further understanding of temporal and spatial distribution of eggs and larvae.

Retention of eggs and larvae near coastal spawning grounds may be favourable to the survival and development of offspring. In general, warm coastal waters tend to be high food production areas encompassing suitable habitat for early life stages of marine fish (Frank and Leggett 1983; Laprise and Pepin 1995). Increased temperature later in the spawning season may result in faster development times, larger larval size-at-hatch and increased survival (Pepin *et al.* 1997). Bradbury *et al.* (2001) also found lower mortality rates and less dispersal with an increase in water temperature for coastal cod in Placentia Bay. However, late spawning and retention of eggs may involve trade-offs between increased hatching success and increased predation or food competition (Economou 1991). Furthermore, larvae spawned earlier in the season may gain a survival advantage by having a larger size at the onset of winter (Grant and Brown 1998; Fortier *et al.* 2006).

Other studies of cod egg distribution in fjord environments have also shown late season concentrations in the inner regions (reaches) of the fjord. Smedbol *et al.* (1998) found the highest egg concentrations in July and August at inner stations in another fjord in Trinity Bay. Smidt (1979) noted a marked increase in egg numbers at innermost stations while conducting plankton sampling in fjords in southwest Greenland. In a study of 20 Norwegian fjords, Knutsen *et al.* (2007) found a regular pattern of decreasing egg density from inner to outer fjord.

In conclusion, the present work provides evidence of multiple spawning peaks over a prolonged spawning season for cod in a coastal inlet. The retention of eggs and larvae in Smith Sound may foster local recruitment, however, eggs and larvae were also advected from the spawning area. A hypothesis is proposed that the different peak

spawning events are indicative of disparate life history strategies (e.g., resident and migratory ecotypes) for cod in Smith Sound.

		stage of development				
		I	II	III	IV	all stages
2006	Mar	0.034	-	-	-	0.034
	Apr	0.316	0.089	0.007	-	0.413
	May	0.075	0.092	0.066	0.007	0.241
	Jun	0.178	0.028	0.009	0.001	0.216
	Jul	0.721	0.302	0.089	0.004	1.116
	Sept	0.041	0.057	0.073	0.025	0.197
2007	Mar	0.023	0.001	-	-	0.024
	Apr	0.161	0.015	0.001	-	0.178
	May	0.078	0.022	0.010	-	0.110
	Jun	0.162	0.032	0.031	0.004	0.229
	Jul	0.962	0.122	0.053	0.004	1.141
	Aug	0.605	0.215	0.096	0.002	0.918

Table 1.1 Monthly mean egg density (egg·m^{-3}) for Smith Sound by stage of development.

Response	Source	SS	df	MS	F	*p* value
log(allstgs)	Year	0.005	1	0.005	0.428	0.514
	Month(Year)	1.567	10	0.157	14.36	<0.001*
	Error	1.179	108	0.011		
log(stg1)	Year	0.023	1	0.023	2.714	0.102
	Month(Year)	1.096	10	0.110	13.053	<0.001*
	Error	0.907	108	0.008		
log(stg2)	Year	0.004	1	0.004	3.623	0.060
	Month(Year)	0.153	10	0.015	12.513	<0.001*
	Error	0.132	108	0.001		
log(stg3)	Year	0.001	1	0.001	1.028	0.313
	Month(Year)	0.036	10	0.004	2.987	0.002*
	Error	0.130	108	0.001		
log(stg4)	Year	0.000	1	0.000	4.574	0.035*
	Month(Year)	0.001	10	0.000	5.248	<0.001*
	Error	0.002	108	0.000		

* Significant at $p<5\%$

Table 1.2 Hierarchical (nested) ANOVA table for log transformed egg density ($egg \cdot m^{-3}$) by stage of development in response to year and month.

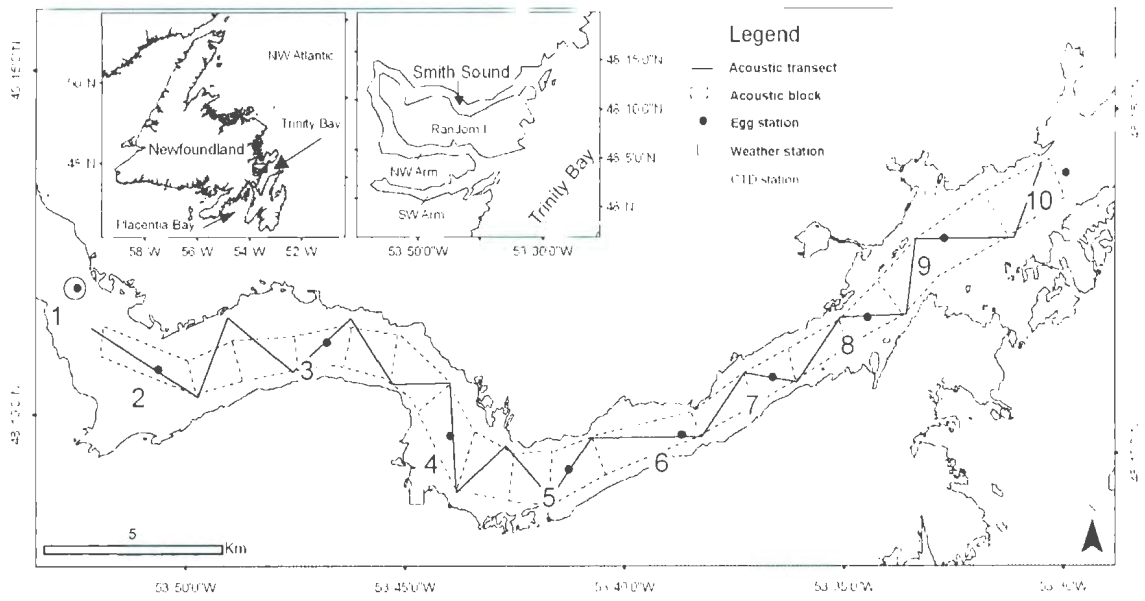

Figure 1.1 Map of study area. Insets show position of Smith Sound relative to Newfoundland and the Random Island area of Trinity Bay. Large map indicates approximate position of acoustic transects (solid line) and egg (numbered black circle) and CTD (open circle) sampling stations.

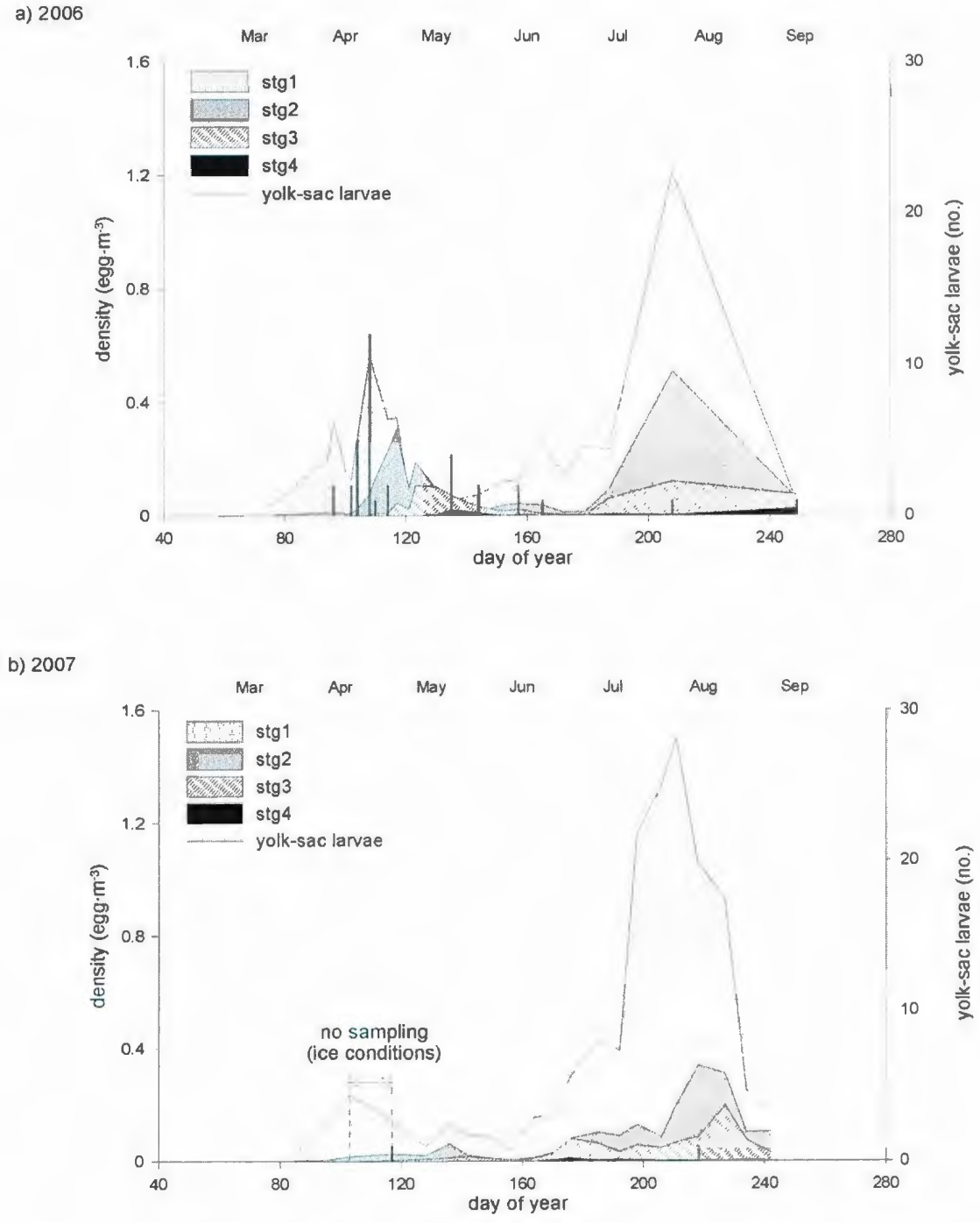

Figure 1.2 Cod egg density by stage of development and number of yolk-sac larvae collected in Smith Sound in 2006 and 2007.

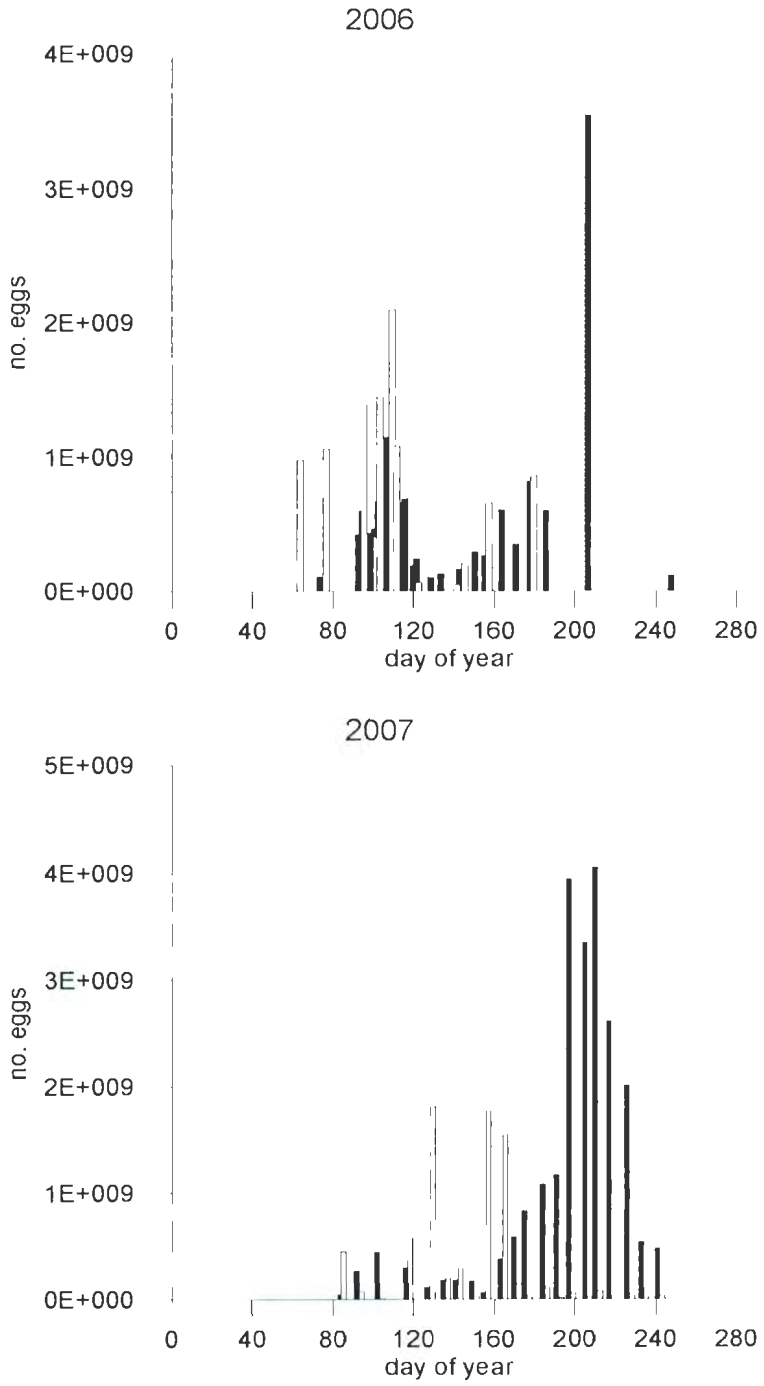

Figure 1.3 Total eggs present in Smith Sound (solid bars) and egg potential estimated from acoustic surveys, maturity state and fecundity (open bars). See text for details on methods used.

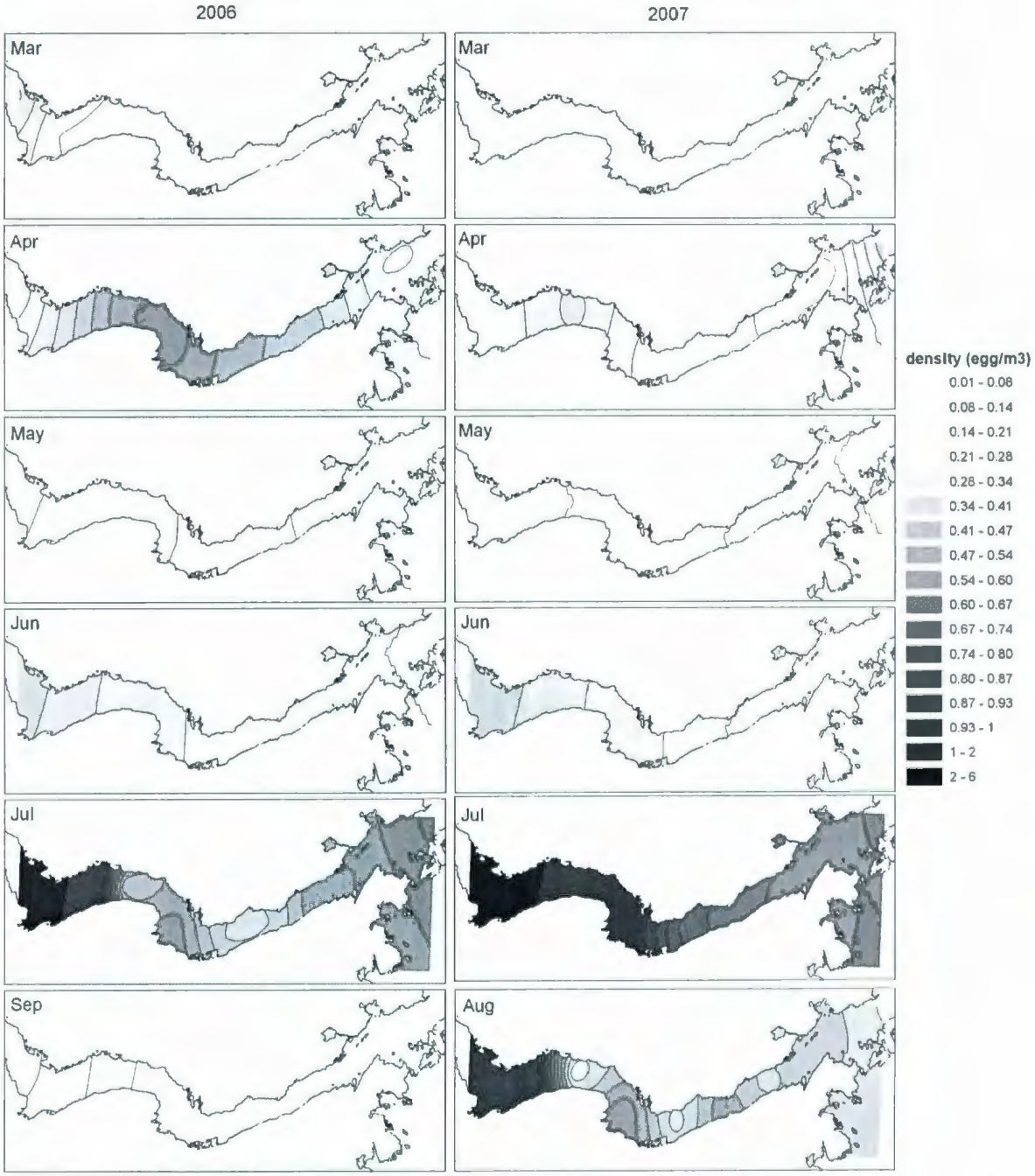

Figure 1.4 Stage I egg abundance and distribution by month

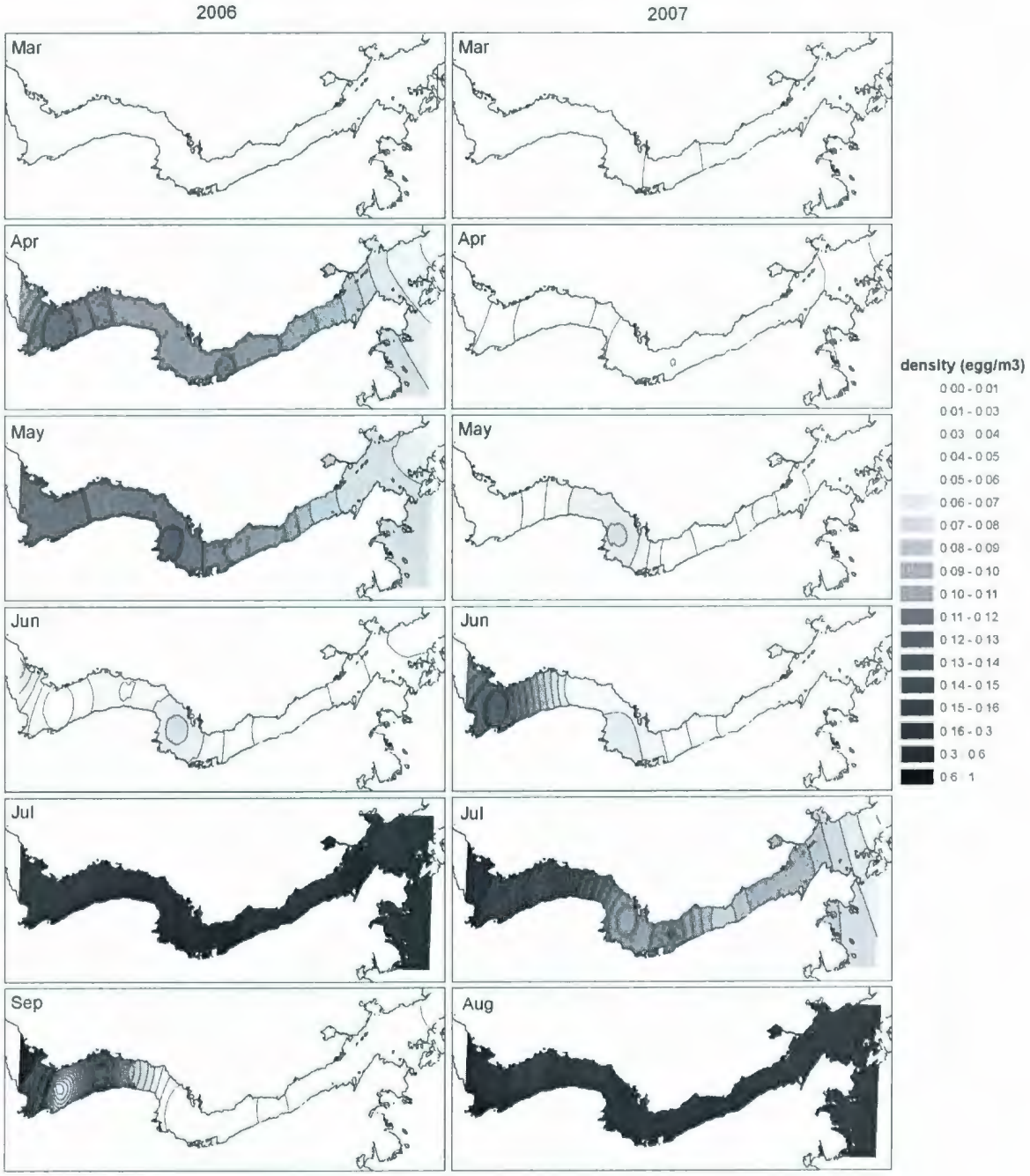

Figure 1.5 Stage II egg abundance and distribution by month

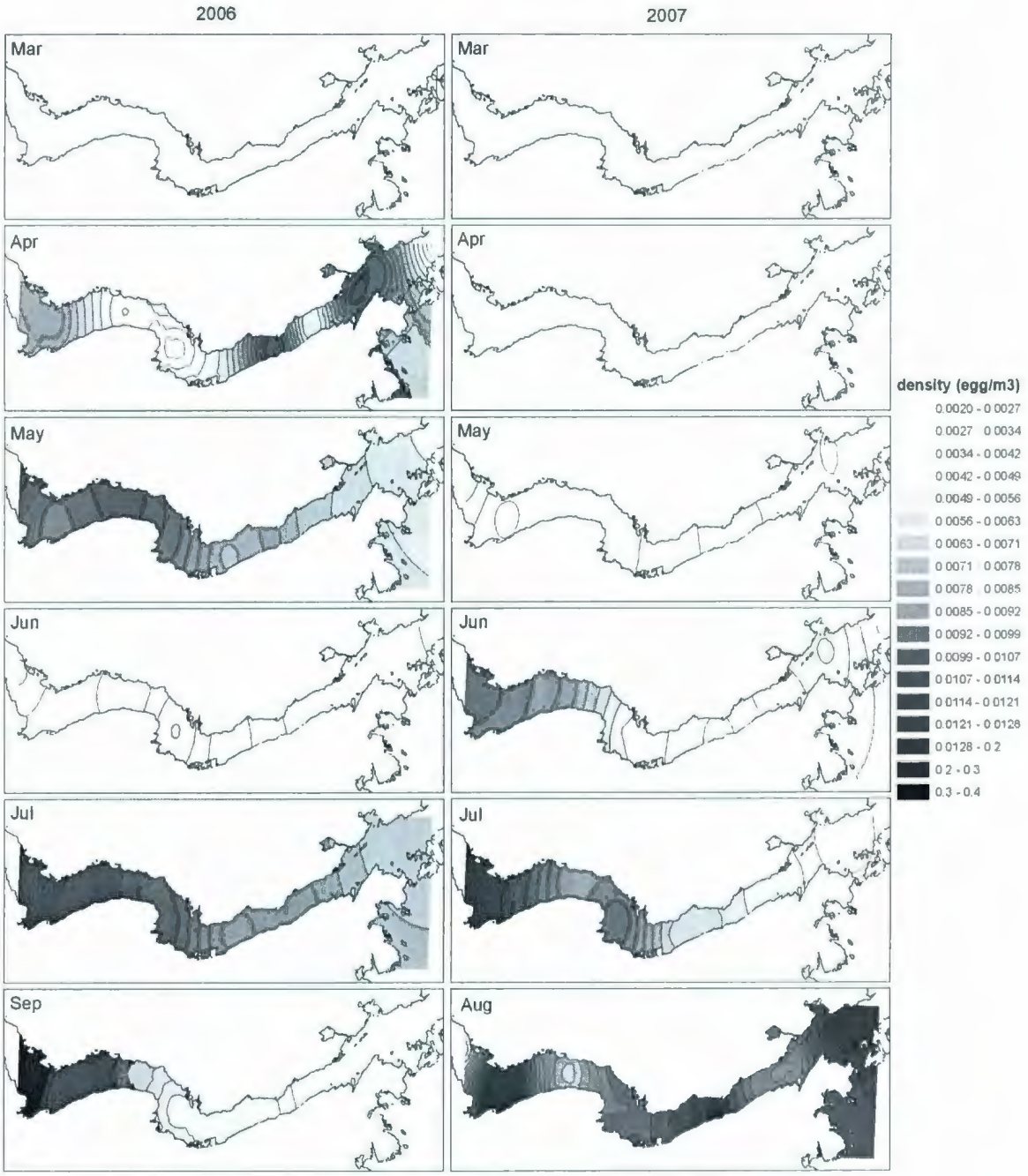

Figure 1.6 Stage III egg abundance and distribution by month

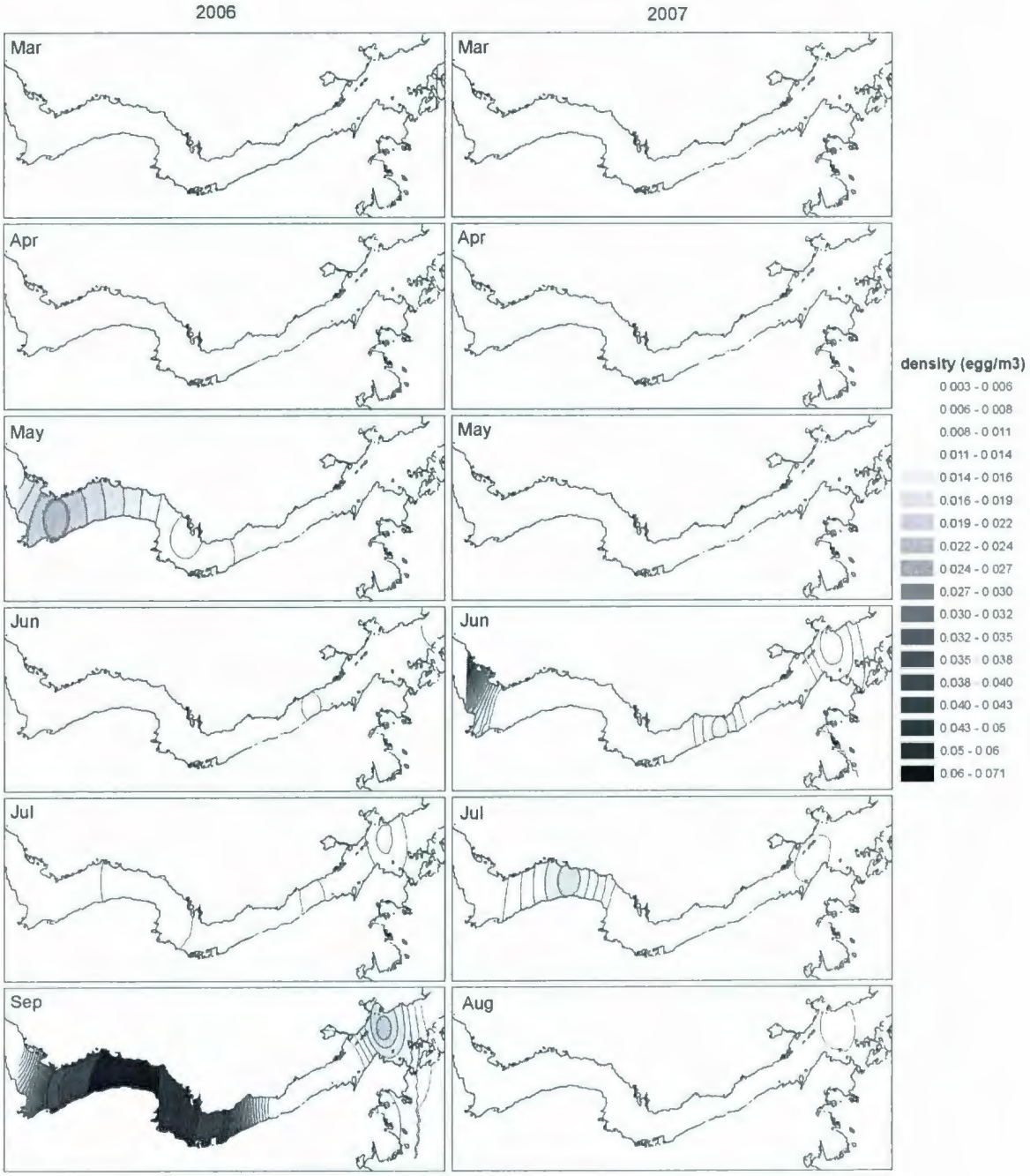

Figure 1.7 Stage IV egg abundance and distribution by month

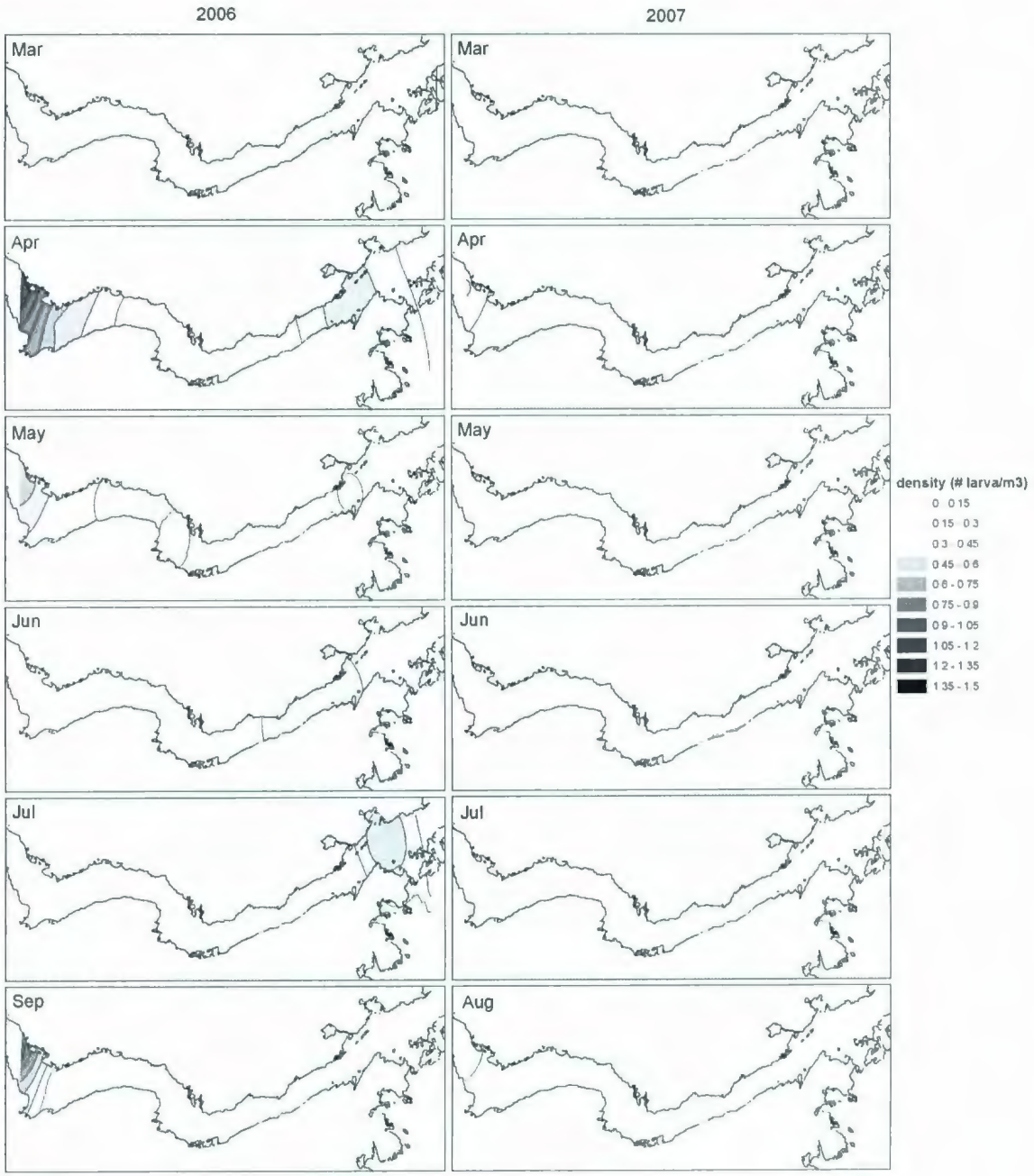

Figure 1.8 Yolk-sac larvae abundance and distribution by month

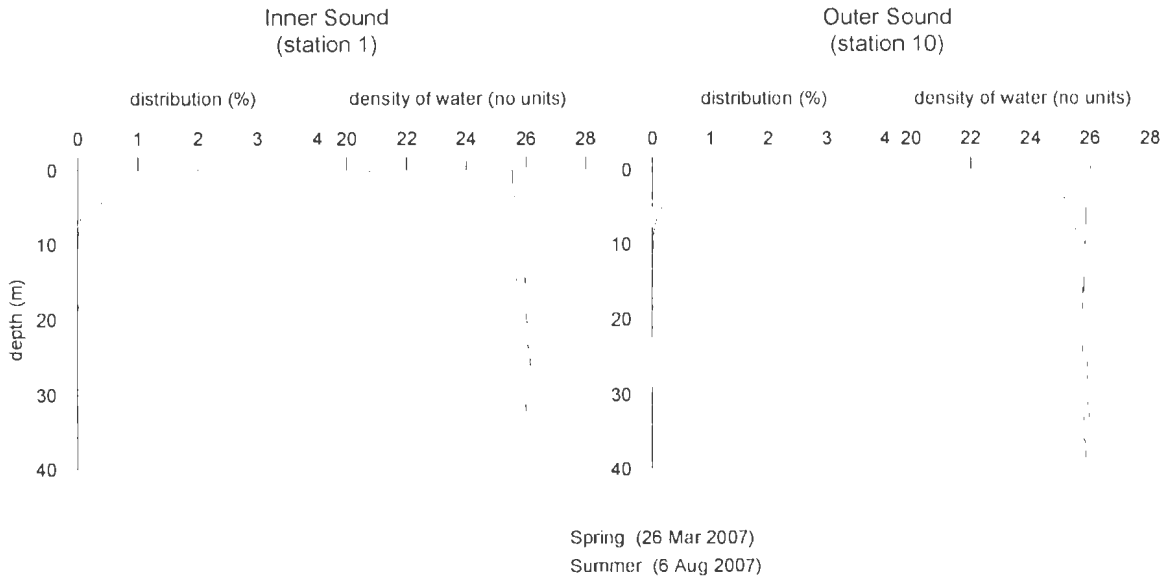

Figure 1.9 Modelled seasonal vertical egg distributions and water density profiles at inner and outer stations in Smith Sound for 2007. See text for methods used.

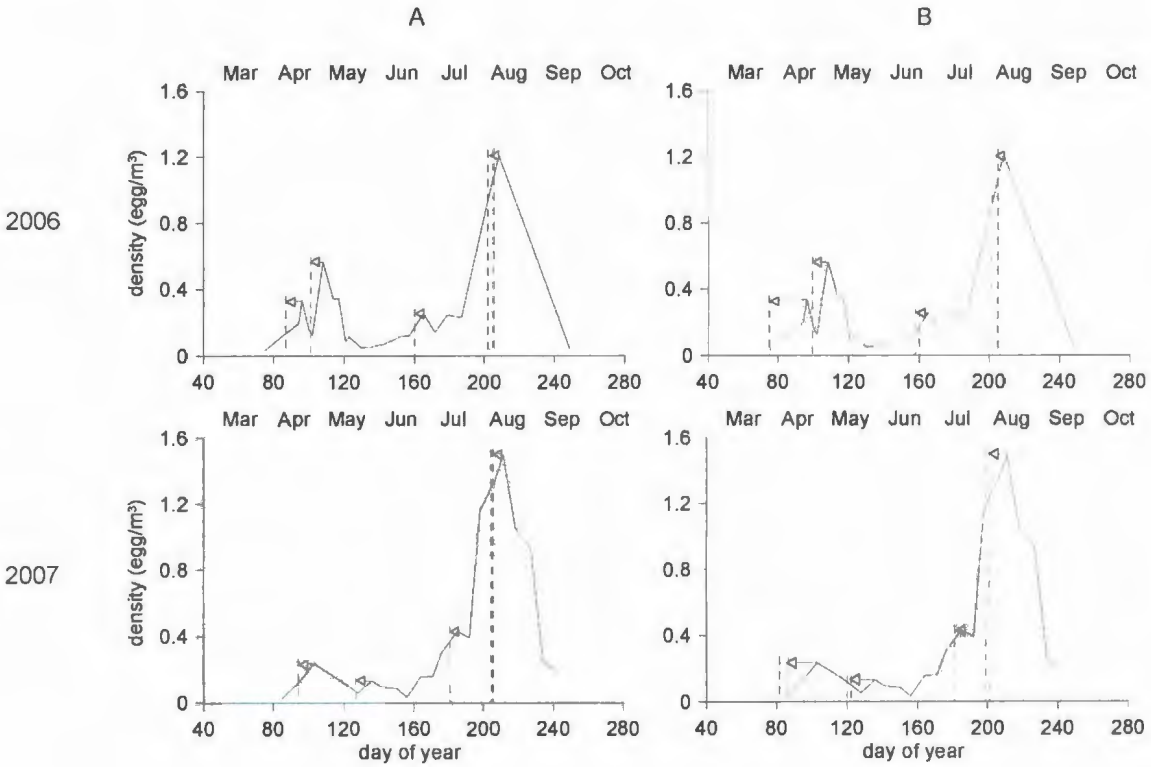

Figure 1.10 Peak spawning times for cod in Smith Sound 2006-2007 backcalculated using temperature dependent development relationships from A) Pepin *et al.* (1997) and B) Page and Frank (1989). In each plot, vertical broken lines represent spawning times backcalculated from peak egg densities (solid line).

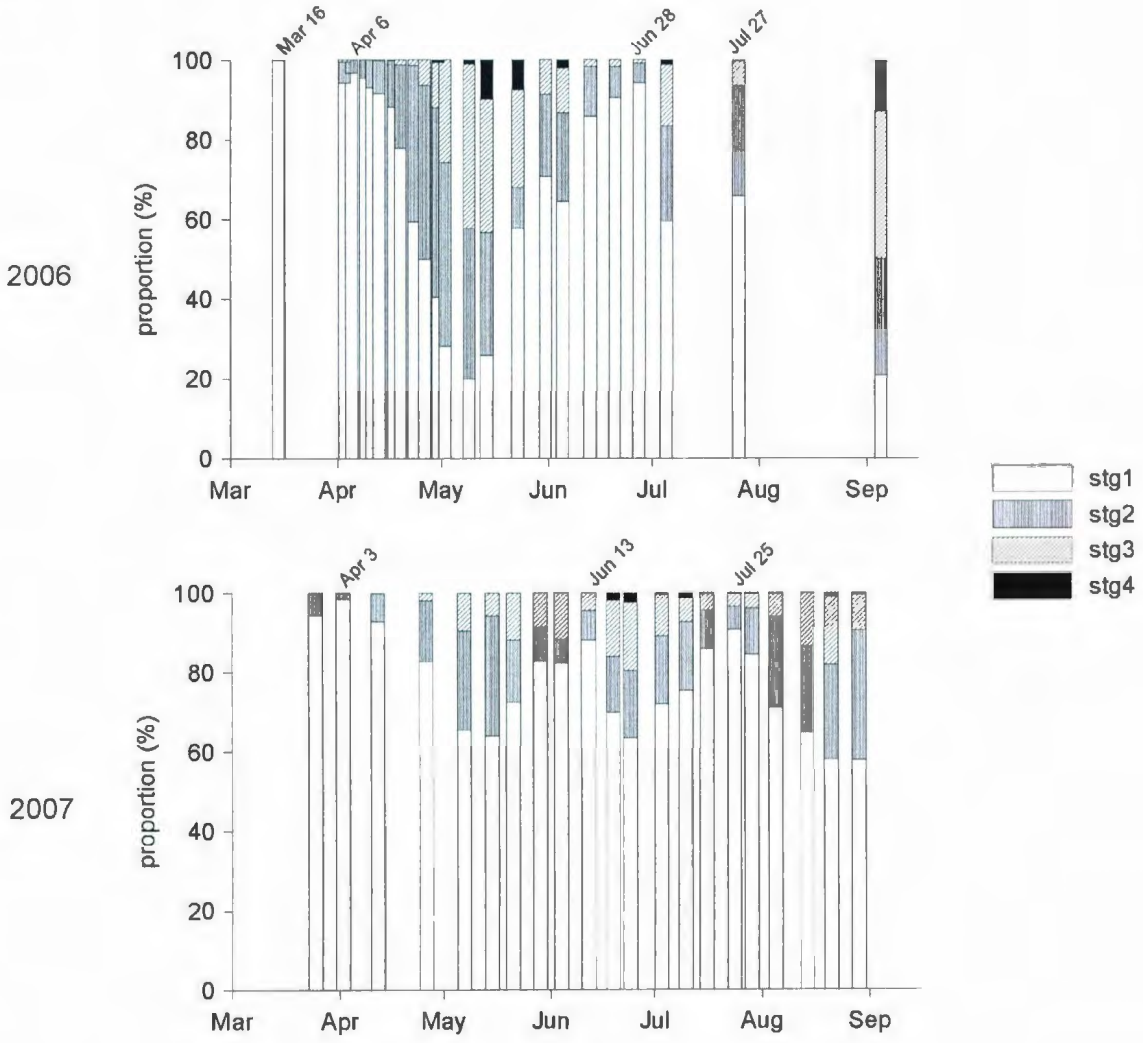

Figure 1.11 Proportion of eggs by stage of development (I-IV) for each survey 2006-2007. Dates indicate times of highest proportion of stage I eggs.

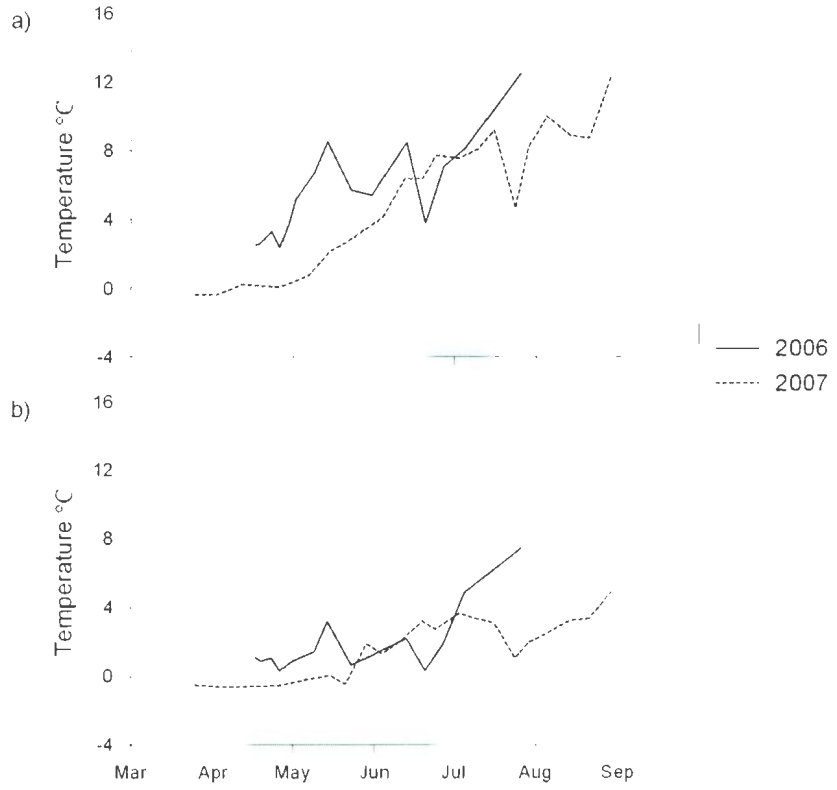

Figure 1.12 Mean a) surface (<5m) and b) mixed layer temperatures (<40m) for Smith Sound in 2006 and 2007

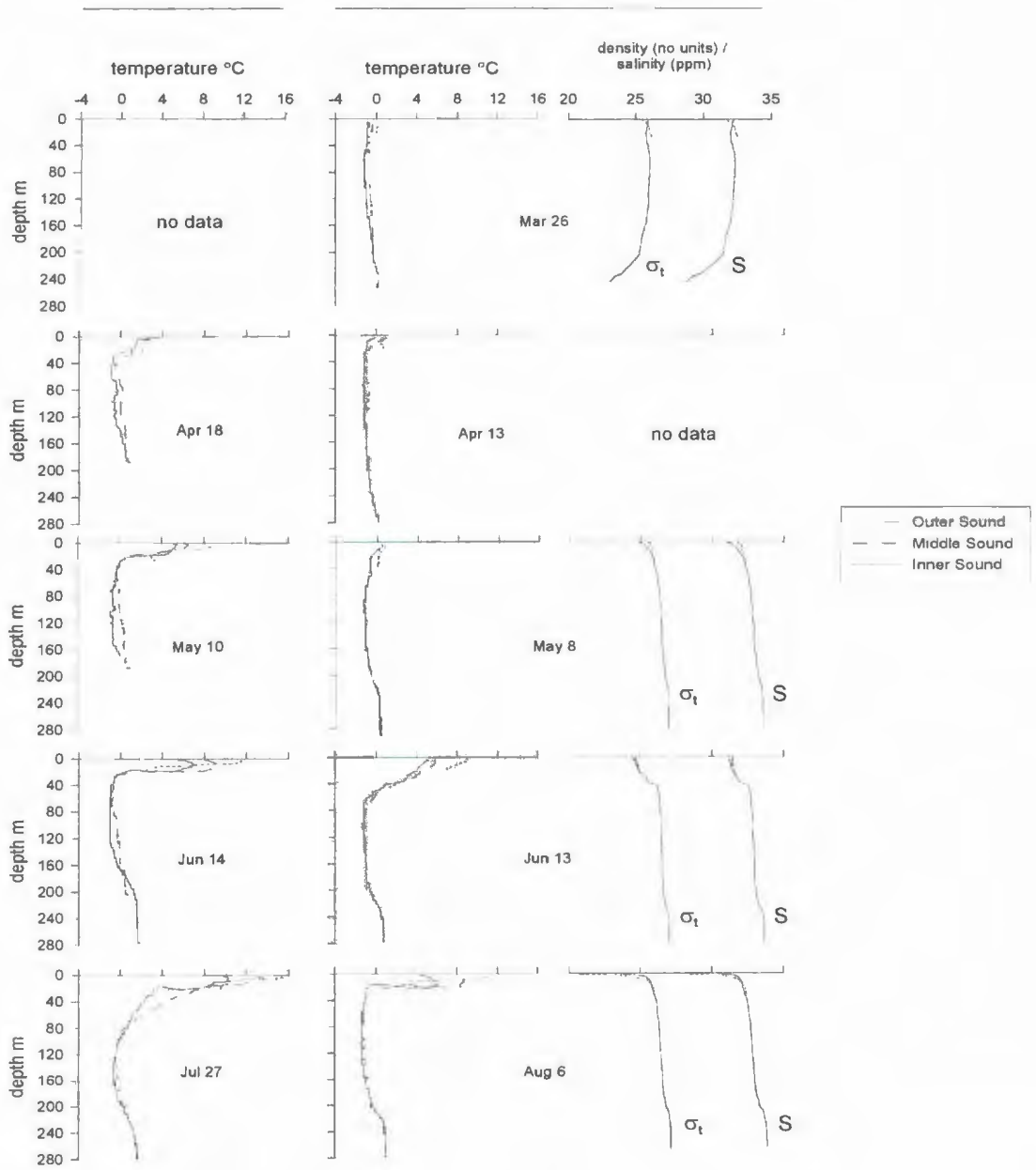

Figure 1.13 Monthly temperature profiles for 2006 and temperature, salinity (S) and density (σ_t) profiles for 2007. In each plot the solid line represents profiles for outer Sound (station 10), hatched line - middle Sound (station 4), and dotted line - inner Sound (station 1). (Note: no density/salinity profiles shown for middle of Sound). See map of study area for station positions.

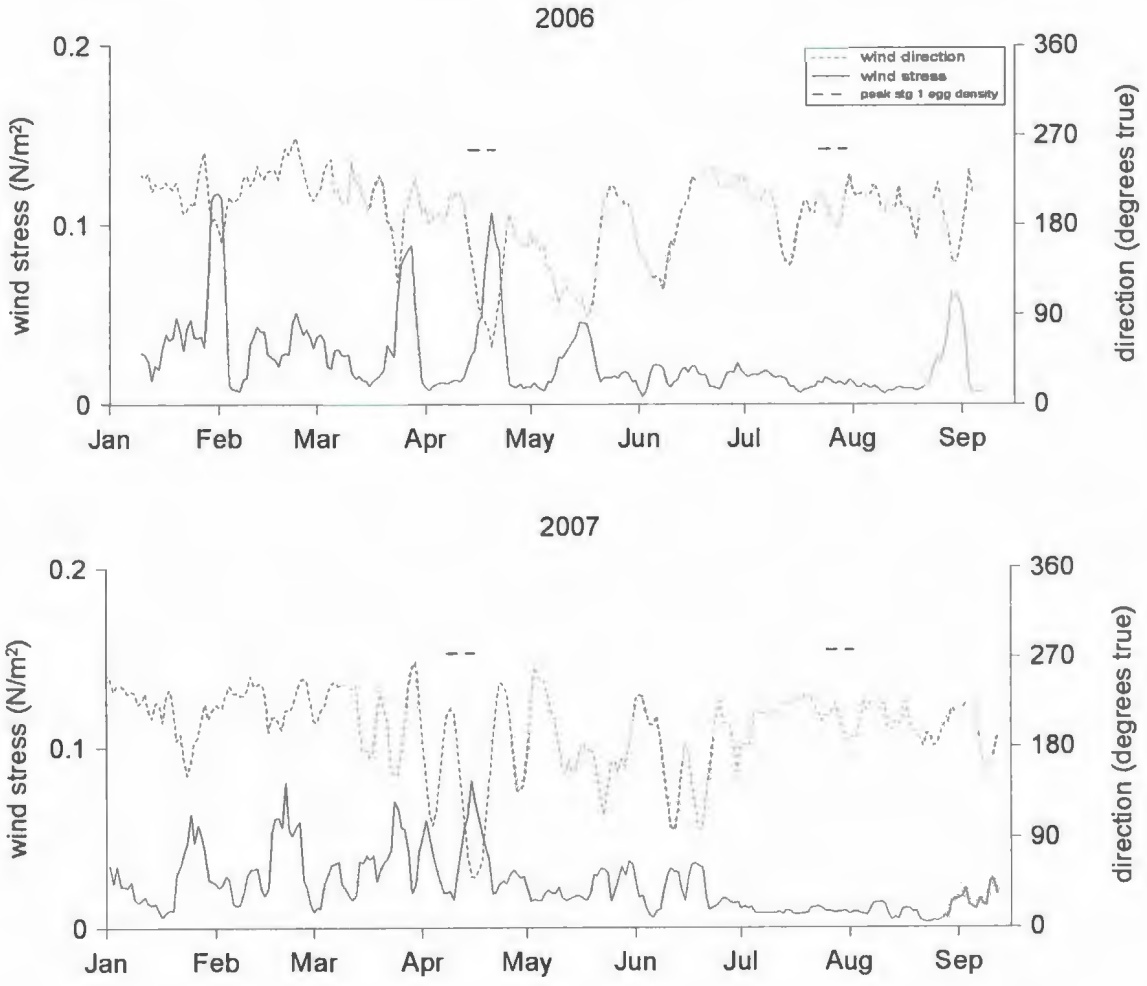

Figure 1.14 Daily mean wind stress (solid line) and direction (dotted line) for study period. Hatched lines indicate periods of highest stage I egg concentrations in the Sound.

Chapter 2. Coincidence of Atlantic cod (*Gadus morhua*) spawning columns and peak egg production in coastal Newfoundland.

2.1 Abstract

Hydroacoustic methods were used to assess the temporal association of specific pelagic behavioural patterns (i.e., 'spawning columns') of Atlantic cod (*Gadus morhua*) with early stage egg density in the coastal spawning area of Smith Sound, Newfoundland in order to test the hypothesis that columns are linked to spawning. Columns were observed during spring in 2006 and throughout the spawning season in 2007. Columns were typically located in sub-zero waters at depths from 60-230 m in the middle of the Sound in March and April, but slightly deeper (100-250 m) and nearer the outer part of the Sound in May and June. Fish density within columns was highest in spring, exceeding 1 $kg \cdot m^{-2}$, decreasing over the spawning season. Columns were observed extending from shoals, in conjunction with pelagic distributions of cod, and as dense pillars of acoustically resolvable individual fish. The frequency and relative size (biomass) of columns coincided with back-calculated spawning times and peaks in early stage egg abundance (4-11 Apr and 21-24 Jul), except for the latter part of 2006 when sampling was limited. This study indicates that pelagic spawning columns were temporally associated with spawning, and that such behaviour can be used as a marker for spawning events.

2.2 Introduction

Atlantic cod (*Gadus morhua*) are marine broadcast spawners that release batches of eggs at intervals over a spawning period that can last 50-60 days (Kjesbu 1989). Brawn (1961) was the first to examine in detail the mating behaviour under laboratory conditions. She observed that males aggressively establish and defend territories (small volumes of water or sections of the enclosure) in a 10.8 m^3 tank, prior to spawning and that courtship behaviour that includes vocalized grunts, circling and fin displays, occurs before and during spawning. Brawn (1961) observed the release of eggs and sperm near the surface of tanks (1.3 m deep) during a ventral mount by the male. Hutchings *et al.* (1999) provided evidence of non-random mate choice in captive cod and concluded that male territorial dominance was linked to body size but in contrast to Brawn's earlier work, observed the discharge of gametes near the bottom of the enclosure (3 m). In free-living cod, pelagic spawning distributions were first observed in Norway using echosounders (Sund 1935). Vertical aggregations termed 'spawning columns' were first described by Rose (1993) on the northeastern Newfoundland shelf; he hypothesized that columns might comprise pairs or small groups of cod engaged in pre-spawning courtship. Since that initial observation, the occurrence of cod columns during spawning events has been reported in other cod stocks (Ouellet *et al.* 1997; Lawson and Rose 2000a; Fudge and Rose in press). It remained unclear, however, what the function of the columns might be and whether these structured aggregations were a component of pre-spawning, was territorial courtship behaviour or were associated with spawning events.

Locating the place and time of cod spawning has typically been accomplished using three methods: 1) analysis of maturation condition data from research trawls (e.g., Hutchings *et al.* 1993; Jakobsen 1987; Marteinsdóttir and Björnsson 1999); 2) acoustic recognition of spawning behaviour (Sund 1935; Boudreau 1992); 3) egg surveys (e.g., Brander 1994; Bradbury *et al.* 2000; Wieland *et al.* 2000); or a combination of methods (e.g., Rose 1993; Ouellet *et al.* 1997; Tomkiewicz *et al.* 1998). Very few studies have attempted to simultaneously describe distributions of spawning adults and propagules (see Rose *et al.* 2008).

In this study, I describe the spatial and temporal patterns of spawning Atlantic cod (*Gadus morhua*) in Smith Sound, Trinity Bay, Newfoundland using concurrent hydroacoustic and ichthyoplankton surveys and maturation sampling over two spawning seasons. Smith Sound contains the largest extant coastal overwintering and spawning component of the once abundant northern cod stock (Rose 2007). Specific objectives of this study were to (1) relate behavioural characteristics of spawning fish to spawning times estimated from egg surveys and (2) quantify spatial and temporal spawning dynamics of cod using egg and acoustic surveys. In particular, I test the hypothesis that specific behavioural patterns (i.e., spawning 'columns') indicated by acoustic echograms would coincide with spawning events as indicated by peaks in early stage cod egg densities and distribution.

2.3 Methods

The study was conducted from 15 January to 6 September 2006 and 13 January to 6 August 2007. Two types of surveys, ichthyoplankton and acoustic, were performed concurrently in most instances after March when ichthyoplankton surveys were initiated. All surveys were run during daylight hours and took <12 hrs to complete (9 hrs if only one of the surveys was conducted). In 2006, both surveys were done approximately every 3 days during the spring in an effort to obtain high resolution data on egg abundance and adult distribution at the onset of spawning, with some egg surveys in the summer without acoustic surveys (cod move in summer to very shallow waters (<50 m) and out of the range of the present acoustic survey). Results from 2006 indicated a broad spawning period with multiple spawning peaks, and as a result, surveys were more evenly distributed over the full spawning period during 2007, with the exception that ice conditions prevented work during a two-week period in April.

2.3.1 Study Area

Smith Sound is a narrow fjord in the western part of Trinity Bay on Newfoundland's northeast coast (inset, Figure 2.1) measuring approximately 22 km in length and 2 km in width. Basin depths within the mid-line trench range from 200 to 350 m and sill depths range from 150 m in the middle and outer Sound to less than 40 m at the innermost portion. Circulation patterns are believed to be controlled by tides, wind forcing and surface inflow from surrounding land (Farmer and Freeland 1983; L. Zedel Dept of Physics and Oceanography, Memorial University of Newfoundland, pers comm).

The Smith Sound cod have been monitored since 1995 and have overwintered and spawned each year in the Sound since then (Rose 2003; 2007).

2.3.2 Acoustic methods

A total of 44 acoustic surveys were carried out between January 2006 and August 2007 from the *RV Coastal Explorer* (14 m) using a Simrad EK 500 echosounder equipped with a 38-kHz, hull-mounted, split-beam transducer. The acoustic system was calibrated using a standard tungsten carbide sphere according to methods detailed by Foote *et al.* (1987). Similar surveys of this area have been conducted since 1995 and are described by Rose (2003). The original survey design was developed to provide acoustic biomass estimates during the winter-spring months when cod aggregate in deep waters along the mid-line of the Sound (Rose 2003). Survey coverage was limited to depths greater than 50 m because cod are likely to display vessel avoidance at shallower depths (Handegard *et al.* 2003; Winger 2004). Cod that remain in the Sound year-round move into warmer, shallower waters (<50m) as temperature increases throughout the spring and summer (Rose 2003, 2007) and will not be detected by this survey, which impacts some interpretation of the results. Briefly, the Sound was divided into blocks according to the bathymetry to a minimum depth of 50 m (Figure 2.1) with each block transversed diagonally at least once at a speed of ~5 knots during each survey. The 50 m limit was set to include all previously observed cod during the winter and spring. In addition, it was likely that at shallower depths, some vessel avoidance might occur (Winger 2004). Vessel avoidance was not a criterion for the initial survey design for cod distributed in much deeper waters, but for summer surveys of cod in depths to 10 m, this is an issue. Raw

acoustic data were edited and integrated to generate areal backscatter (s_A) values using Echoview 4.0 and 4.3. Backscattering data (s_A) were arranged in 100 m bins along transects and converted to areal fish density ($kg \cdot m^{-2}$) using a target strength (TS) model from Rose (2003) with command scripts written for SYSTAT 12.

1) TS (dB/kg) = -11.26 log length (cm) -13.67

based on weight (kg) = 0.0005 length $(cm)^{3.126}$ and TS (dB/fish) = 20 log length (cm) - 67.5. Fish density ($kg \cdot m^{-2}$) was extrapolated to block area to estimate biomass within the block using spherical kriging analysis in *GS+* geostatistical software. Mean fish length and weight, and other biological data including maturation stages were determined from limited cod catches over the course of the study (fishing in this area, especially with bottom trawls, is a sensitive issue and must be done conservatively). Fish were sampled mostly from trawl catches from the *CCGS Shamook* except for June 2006, when cod were caught using feathered hooks and hand lines from the *RV Coastal Explorer*. Total length, weight, sex and spawning condition were recorded for each fish. Stage of maturity was determined from visual examination of gonads based on classification from Morrison (1990). Historical catch data from previous trawl surveys (primarily DFO fall research bottom-trawl surveys) were used to supplement biological data collected during the study period.

Spawning 'columns'(Rose 1993, Lawson and Rose 2000a) were discerned from visual interpretation of acoustic echograms and defined and integrated using Echoview Schools Module. Only vertical aggregations (groupings of cod with a much larger height

to width ratio) at least 10 m in height were classified as spawning columns and thus used in analyses. Areal fish density ($kg \cdot m^{-2}$) and area (m^2) were extracted and combined to give an estimate of the biomass of columns:

2) $\quad Biomass\ (kg) = D\ (kg \cdot m^{-2}) \times A\ (m^2)$

A relative behavioural index defined as the proportion of biomass (t) in columns relative to the total biomass estimated for each survey.

2.3.3 Egg Surveys

Methods for egg collection and analysis are described in detail in section 1.3.2 of Chapter 1.

2.4 Results

2.4.1 Acoustics

Cod were detected hydroacoustically throughout the study period. As in previous years (see Rose 2003; 2007), cod over-wintered in dense aggregations in the deep waters of the Sound and began spawning in March. Distribution shifted during spring and early summer, with some fish (likely the majority) migrating out of the Sound, while others stayed within the Sound but moved into shallower waters (Rose 2007).

Vertical aggregations of cod or spawning 'columns' were observed in spring in both years and throughout most of the 2007 sampling season, peaking in March-April in 2006 and late April and late July in 2007 (Figure 2.2). Only two acoustic surveys were run between July and September in 2006, hence it is possible that peaks in late season spawning behaviours were missed. Fish density within columns ranged from 0.002 to 0.809 $kg \cdot m^2$ in 2006 and 0.001 to 1.597 $kg \cdot m^2$ in 2007 (Table 2.1) and varied significantly between years as well as among months within years (Table 2.2). Mean column density for each survey was highest in early spring 2007 as cod began to break from overwintering aggregations (e.g., Figure 2.3.1), and tended to decrease over time (Figure 2.4a). Column height was generally between 15-20 m but columns up to 85 m high were observed (Figures 2.3.1-2.3.3). Mean areal density and height were correlated (Pearson correlation, $r=0.238$, $n=274$, $p<0.01$). Columns were observed at depths ranging from 60-235 m but were most commonly observed in 150-200 m of water (Table 2.1, Figures 2.3.1-2.3.3 and 2.4c). Neither column height nor column depth showed statistical variation among months or between years (Table 2.2). Columns were located throughout the study area, but were generally found in deep water near the middle of the Sound in spring and close to the outlet of the Sound into Trinity Bay later in the year (Figure 2.5). One small column was recorded at shallow depths near station 3 in August, 2007.

2.4.2 Adult sampling

A total of 442 cod (221 males, 221 females) were sampled during the course of the study. Fish size ranged from 33-122 cm. Of the 442 fish, 120 were mature females in spawning condition in June (no data beyond June) (Figure 2.6). Longer term data series

from the Sound (n=2124 mature females) from 1997-2004 indicated very few spawning fish in January whereas 5-10 % of mature females had hydrated eggs and thus were judged to be spawning during April and June. The 2006 and 2007 data suggest a somewhat higher proportion of spawning females later in the season (40% in June 2006, and 28.3 % in May 2007).

2.4.3 Egg surveys

Results of the spatial and temporal distribution of all stages of development used for staging cod eggs are reported in sections 1.4.1 and 1.4.2 of Chapter 1. In this chapter, only the distribution patterns of early stage (stage I) eggs are used to provide estimates of adult spawning time and location within the Sound and are of interest.

2.4.4 Temperature

Mean surface and mixed layer water temperatures, as well as temperature profiles at positions in the Sound during the study are reported in section 1.4.4 of Chapter 1. Temperature profile data from the inner and outer study area are used in this chapter to show vertical positioning of spawning columns in the water column relative to temperature (Figure 2.7).

2.4.5 Time of spawning

Results of backcalculated spawning times from mean water temperature and dates of highest stage I egg abundance are reported in section 1.4.3 of Chapter 1.

2.4.6 Coincidence of columns and egg-peak determined spawning times

Peaks in observation of spawning columns coincided with backcalculated peak spawning times in most instances (Figure 2.8). The major exception occurred in summer of 2006 when no columns could be observed as a consequence of lack of surveys. Egg and column distributions were similar in spring (Mar-Apr) of both years but more inconsistent later in the summer. For example, cod eggs were most abundant at the inner parts of the Sound in summer (Jul-Aug) at times when columns were either absent, as in 2006, or frequently observed at the outer parts of the Sound, as in 2007 (Figure 2.5).

2.5 Discussion

In this study, acoustically observed vertical shoaling behaviour by Atlantic cod corresponded with spawning times derived from peaks in early stage cod egg abundance, providing support for the hypothesis that such 'columns' are temporally associated with cod spawning in the wild based on Brawn's (1961) observations of substantial vertical movement by both male and female cod during spawning in the laboratory.

Rose (1993) originally suggested that the observed 'columns' might be composed of pairs of spawning cod. In the present study, the coincidence of columns and egg production predictions confirms that spawning (release of eggs) is occurring during, or near the time of, these formations. However, the present data do not allow the conclusion that spawning is taking place within the columns. The most common male-female interactions in lab studies ('ventral mount' and circling bouts) (Brawn 1961; Hutchings *et*

*al.*1999) were infrequent relative to male-male interactions during the pre-spawning period. Moreover, the most common behaviour between males during pre-spawning is a form of circling, which could explain vertical formations observed in this and previous studies if fish were rising vertically. Hence, it cannot be ruled out that columns may be made up of male cod engaged in agonistic behaviour toward other males prior to spawning, or male cod that have established territories in the vertical plane bordered by sub-dominant or smaller satellite males. Data on the sex composition of the columns is needed to answer this question.

The current study extends previous observations of spawning columns to full spawning seasons in coastal Newfoundland. Studies in other regions have also reported pelagic spawning behaviour (Sund 1935; Plikshs 1990; Rose 1993; Ouellet *et al.* 1997) to the water surface (Templeman 1958; Brawn 1961). Nevertheless, it is not clear if all cod stocks exhibit such behaviour. Variations in spawning behaviours among populations are possible.

Columns generally were 10-20 m in height but exceeded 50 m occasionally (10 m was used as a minimum based on visual observations of many echograms). Column structure varied; some extended from dense shoals (Figure 2.3.1), particularly in early spring, while others appeared densely 'stacked' (Figure 2.3.2) or above loose aggregations (Figure 2.3.3). The high densities within columns observed in spring and subsequent decrease throughout the spawning season was likely related to density declines (cod are highly aggregated in winter-spring and less densely distributed in summer) (Rose 2003; 2007). Columns and most cod at the time of spawning were consistently situated in water temperatures below 0°C (Figure 2.8) confirming that cod in

coastal Newfoundland may spawn at sub-zero temperatures (Smedbol and Wroblewski 1997; Lawson and Rose 2000a).

Column densities measured over area were correlated with column height regardless of season, which suggests volumetric densities were relatively stable. Volumetric fish densities within columns rarely exceeded 0.03 fish·m^{-3} and were comparable but somewhat lower than densities (>1.0 fish·m^{-3}) reported by Lawson and Rose (2000) for southern Newfoundland cod.

Predictions from both methods used to backcalculate spawning times from egg presence match closely the presence of columns later in the season when water temperatures were >2 °C (when data were available). The discrepancy in incubation times at lower temperatures (<2 °C) between the two methods can be partly attributed to methodological differences used to develop these relationships. Pepin *et al.* (1997) conducted a laboratory-based study using a single broodstock, whereas Page and Frank (1989) used literature data from studies on free-living cod and haddock (*Melanogrammus aeglefinus*), and different staging schemes were used to separate egg development stages. There was a better match between the longer development times estimated by Page and Frank (1985) for lower temperatures than with those of Pepin *et al.* (1997), but this may be fortuitous, as a result of a lack of data on development times at temperatures <2 °C (Pepin *et al.* 1997, Geffen *et al.* 2006).

It is believed that spawning is likely to have occurred in summer in waters shallower than 50 m (the limit of the present acoustic surveys) and would have been missed in the present study. Substantiated spawning of cod in waters <50 m deep has been observed in other bays in Newfoundland, as were spawning columns (Lawson and

Rose 2000). Of interest, columns were observed in shallow water (<30m) in early July 2006 in the Sound from a smaller research vessel (7 m) equipped with a scientific echosounder during a related study (Figure 2.10).

In conclusion, this study provides the first quantified measurements of cod spawning 'columns' throughout a spawning season and confirms that these vertical formations are associated with reproductive behaviour in the wild. The behavioural function and composition of these structures requires further study.

			density ($kg \cdot m^{-2}$)			height (m)			depth (m)		
year	date	n	min	max	Mean	min	max	mean	min	max	mean
2006	13-Mar	29	0.008	0.184	0.050	9.5	44.0	17.3	131	232	195
	16-Mar	55	0.005	0.809	0.066	10.0	45.6	17.0	150	205	179
	04-Apr	18	0.002	0.290	0.090	9.1	85.6	28.9	159	204	180
	10-Apr	9	0.010	0.051	0.026	10.9	25.0	13.2	60	109	86
	12-Apr	12	0.002	0.094	0.037	10.5	14.4	10.0	95	175	140
	18-Apr	9	0.004	0.238	0.052	10.2	30.4	14.2	81	96	87
2007	06-Feb	1	0.166	0.166	0.166	17.4	17.4	17.4	180	180	180
	26-Mar	22	0.014	0.746	0.273	10.8	59.6	19.2	155	240	184
	27-Apr	15	0.014	1.597	0.396	10.8	32.0	20.4	134	211	171
	08-May	7	0.042	0.221	0.109	9.5	33.7	15.4	97	134	112
	22-May	2	0.013	0.062	0.038	14.2	24.4	19.3	214	221	218
	30-May	4	0.014	0.074	0.045	9.8	23.0	13.3	181	222	199
	20-Jun	3	0.022	0.033	0.028	9.8	20.0	14.3	198	205	202
	04-Jul	3	0.016	0.063	0.042	16.2	28.0	21.5	190	209	199
	17-Jul	18	0.006	0.046	0.022	9.7	33.0	17.8	175	248	203
	25-Jul	12	0.002	0.042	0.016	10.8	40.0	16.2	146	228	161
	30-Jul	39	0.003	0.053	0.016	9.7	52.8	19.1	134	234	166
	06-Aug	7	0.001	0.038	0.013	12.3	30.0	13.2	138	235	209
	15-Aug	13	0.002	0.019	0.009	10.2	21.8	14.0	152	226	183

Table 2.1 Range and mean density, height, and depth of spawning columns observed in Smith Sound during study period.

Response	Source	SS	df	MS	F	*p* value
density	Year	0.024	1	0.024	39.258	0.000
	Month(Year)	0.169	7	0.024	40.198	0.000
	Error	0.006	10	0.001		
height	Year	0.867	1	0.867	0.031	0.864
	Month(Year)	62.955	7	8.994	0.321	0.928
	Error	280.362	10	28.036		
depth	Year	2939.114	1	2939.114	2.044	0.183
	Month(Year)	6358.549	7	908.364	0.632	0.721
	Error	14377.080	10	1437.708		

Table 2.2 Hierarchical (nested) ANOVA table for mean density, height and depth of spawning columns in response to month and year.

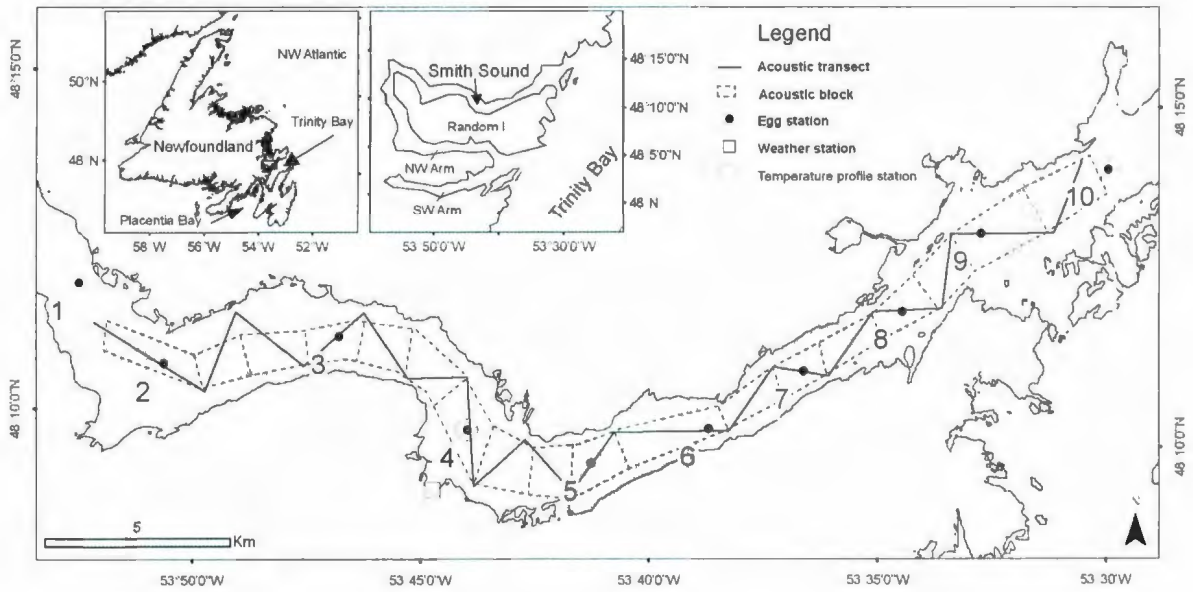

Figure 2.1 Map of study area. Insets show position of Smith Sound relative to Newfoundland and Random Island area of Trinity Bay. Large map indicates approximate position of acoustic transects (solid line), acoustic blocks based on bathymetry (broken line), egg sampling (black circle) and temperature profile stations (open circles).

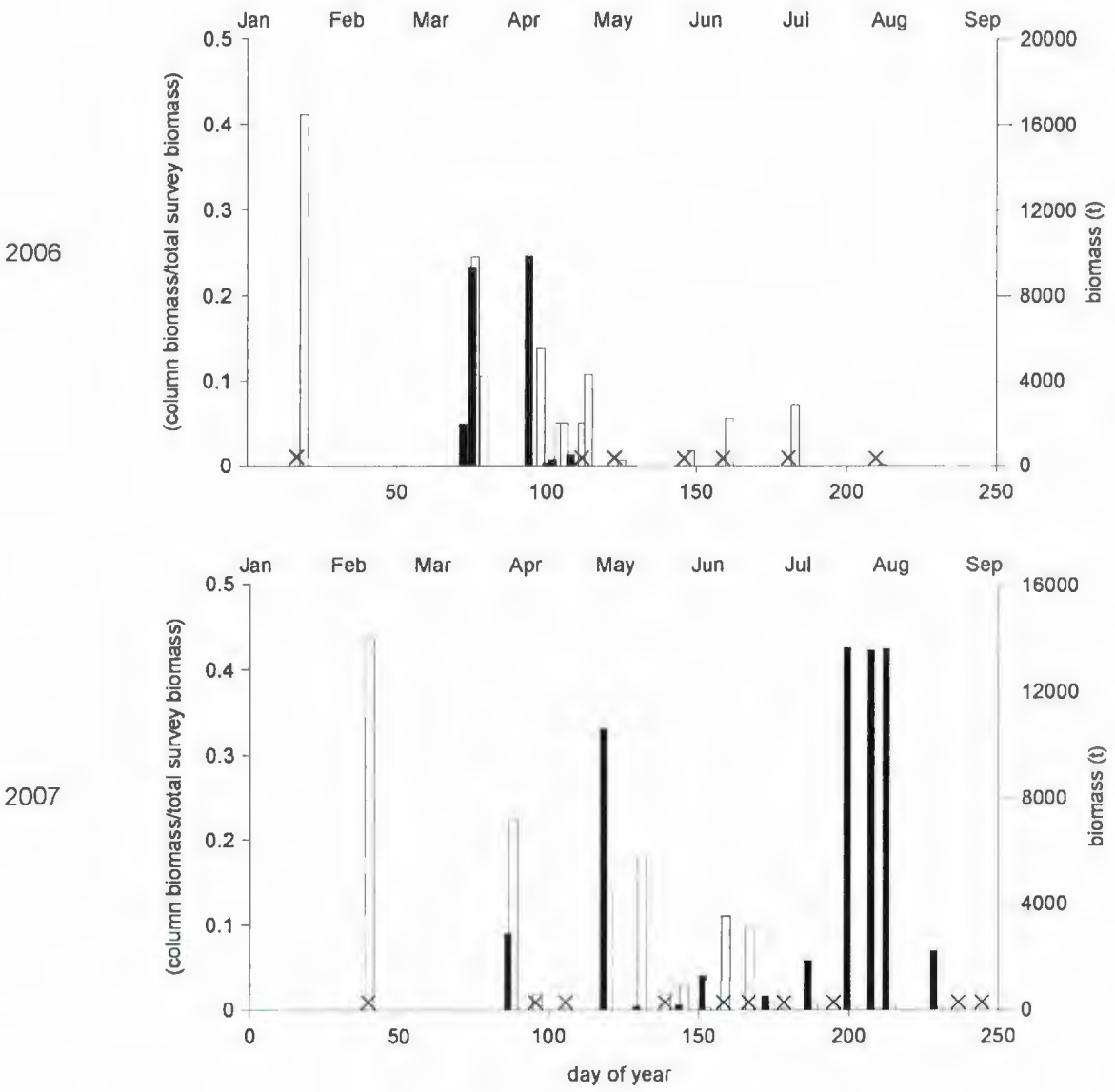

Figure 2.2 Proportion of vertically aggregated behaviour (i.e., spawning columns) (black bars) and total biomass estimated from acoustic surveys (white bars) in study area for 2006 and 2007. Surveys in which no columns were observed indicated by X.

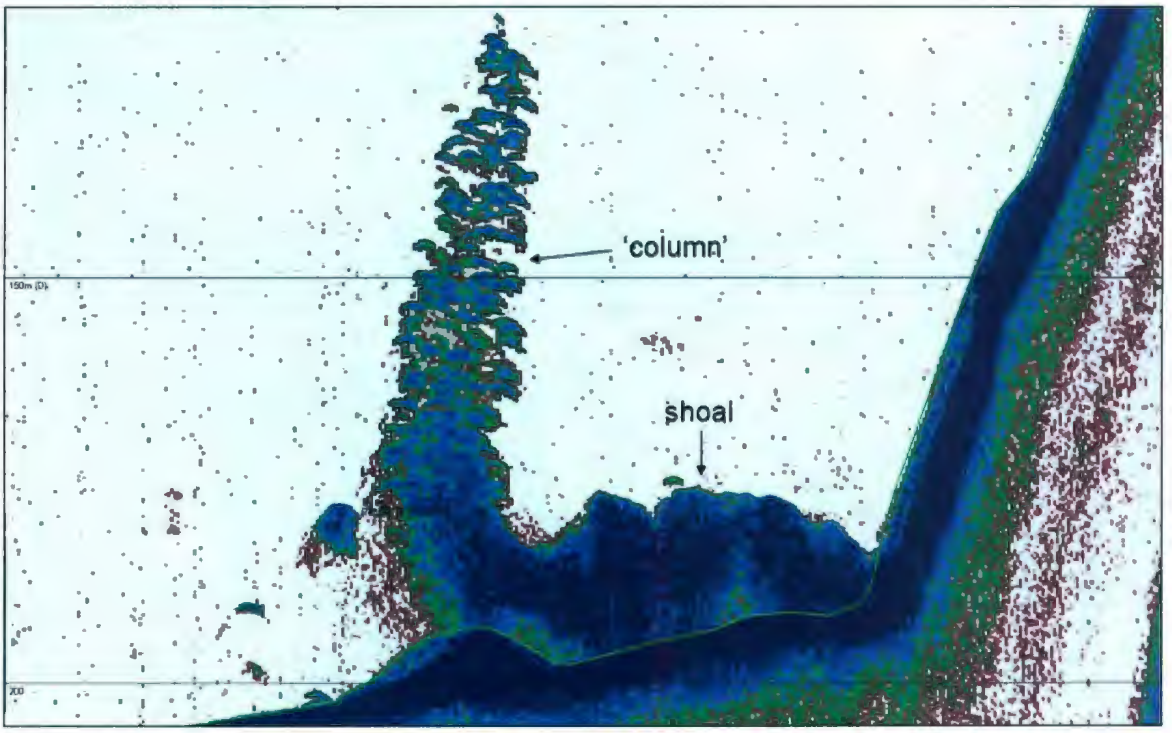

Figure 2.3.1 Acoustic echogram of spawning column extending vertically from dense shoal of cod on 25 March, 2007. Horizontal lines indicate 150 and 200 m depths, echogram spans approximately 2.0 km. The dark blue line represents the bottom. Colour scales are -36dB (dark blue) to -75 (brown).

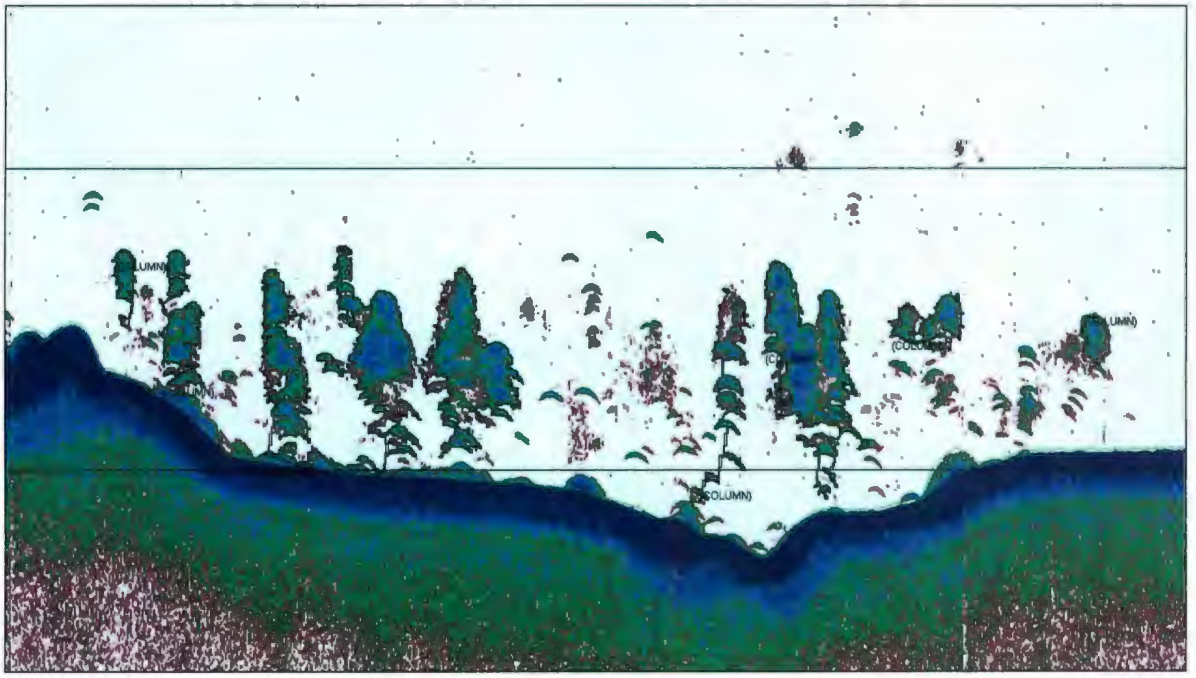

Figure 2.3.2 Acoustic echogram of adjacent 'stacked' spawning columns on 16 March 2006. Horizontal lines indicate 150 and 200 m, echogram spans approximately 1.9 km. The dark blue line represents the bottom. Colour scales are -36dB (dark blue) to -75 (brown).

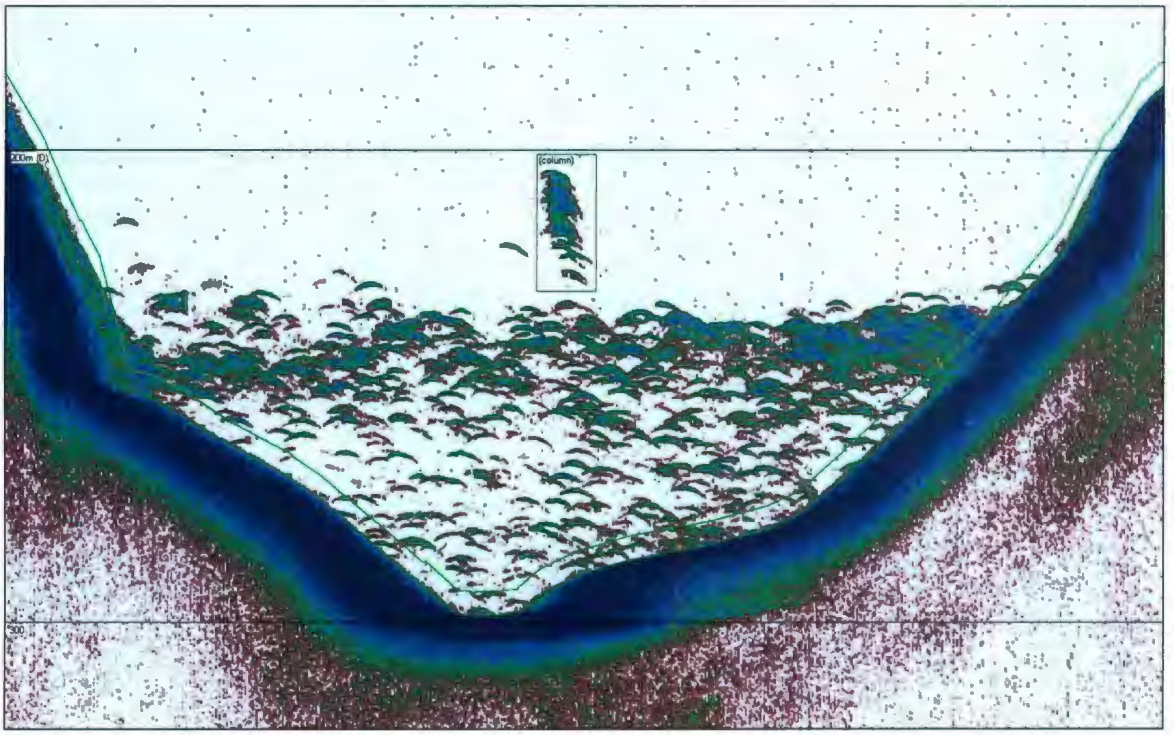

Figure 2.3.3 Acoustic echogram showing single pelagic spawning column above a loose aggregation of cod on 22 May 2007. Horizontal lines indicate 200 and 300 m, echogram spans approximately 1.6 km. The dark blue line represents the bottom. Colour scales are -36dB (dark blue) to -75 (brown).

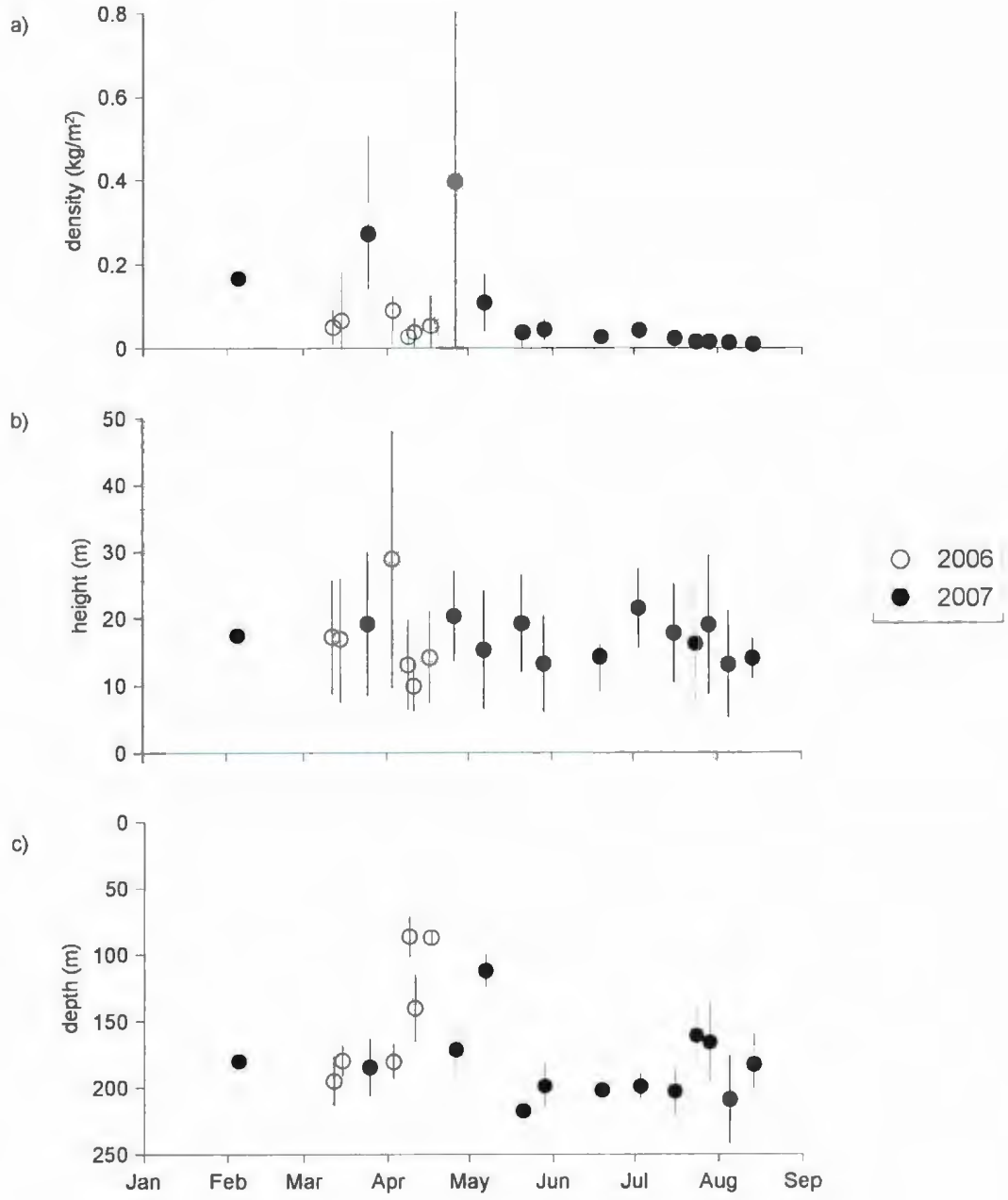

Figure 2.4 Mean ± S.D. for a) density, b) height, and c) depth of spawning columns observed over the study period.

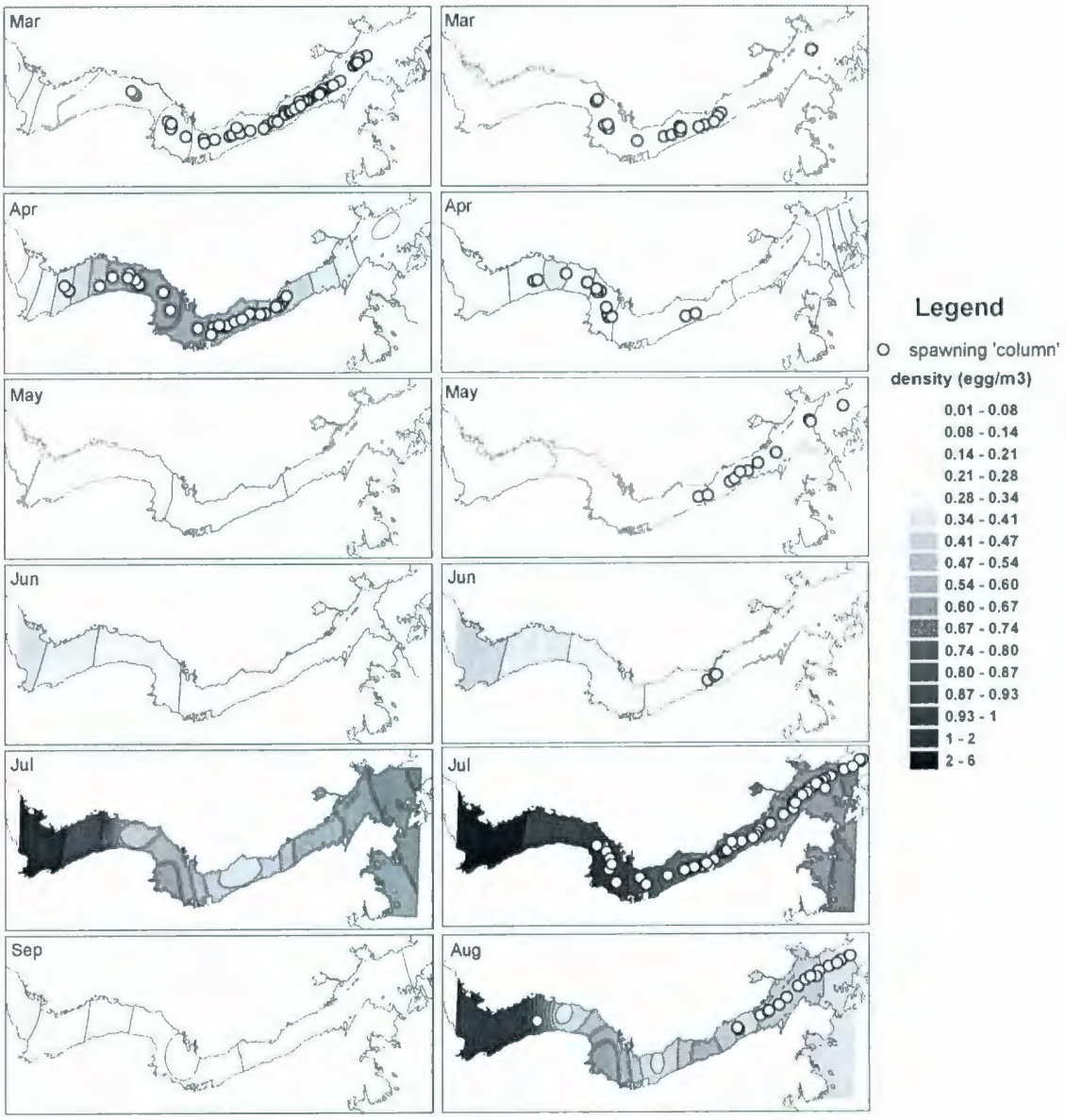

Figure 2.5 Distribution of spawning columns in relation to stage 1 cod egg distribution by month for 2006-2007.

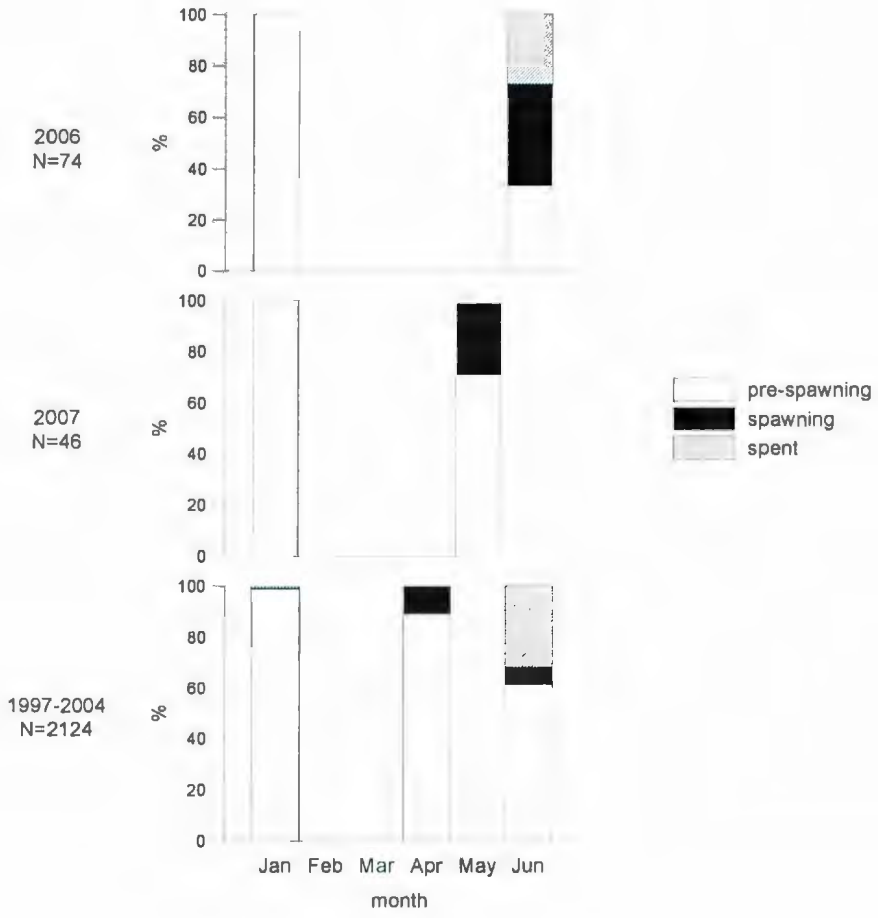

Figure 2.6 Stage of maturation for female cod sampled in Smith Sound in 2006, 2007, and 1995-2005. See text for details on sampling and staging methods.

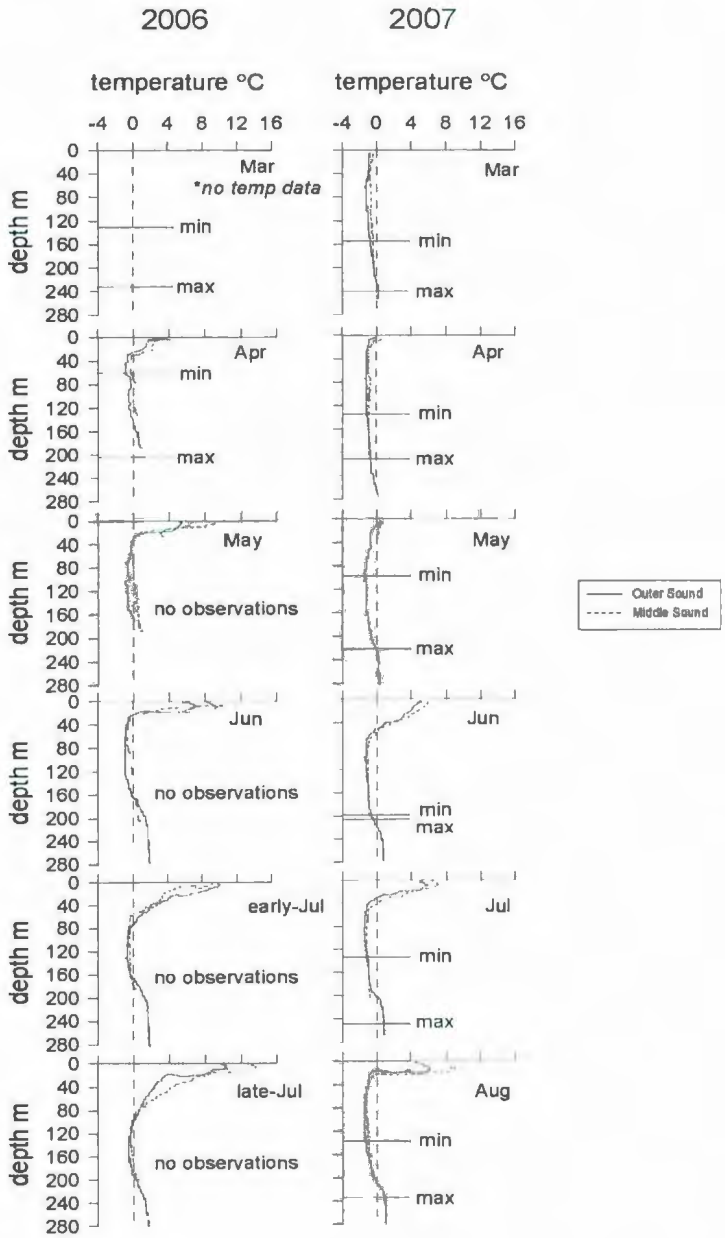

Figure 2.7 Monthly temperature profiles for outer (solid line) and middle Sound (broken line) in relation to vertical distribution of columns in 2006 and 2007. In each plot the solid horizontal lines indicate the minimum and maximum depths at which columns were observed for that month and the hatched vertical line indicates 0°C.

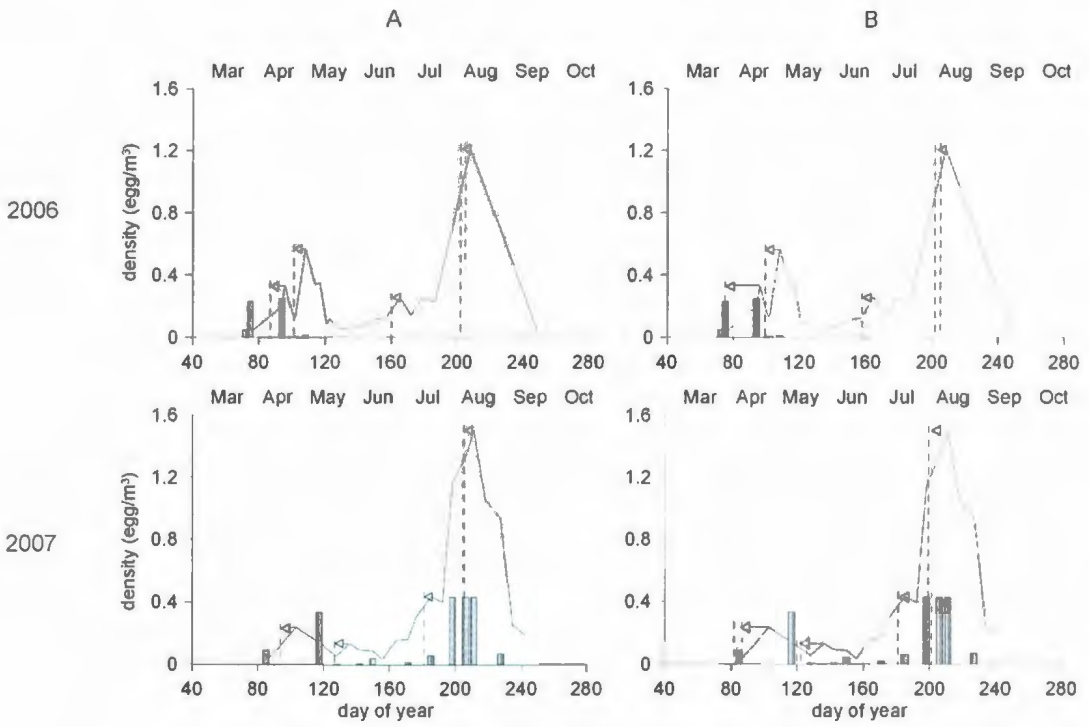

Figure 2.8 Coincidence of peak spawning times from peaks in egg abundance and acoustic observations of spawning behaviour for cod in Smith Sound 2006-2007. Vertical broken lines represent spawning times backcalculated from peak egg densities (solid line) using temperature dependent development relationships from A) Pepin *et al.* (1997) and B) Page and Frank (1989). Vertical bars represent acoustic observations of spawning behaviour as a percentage of the total biomass.

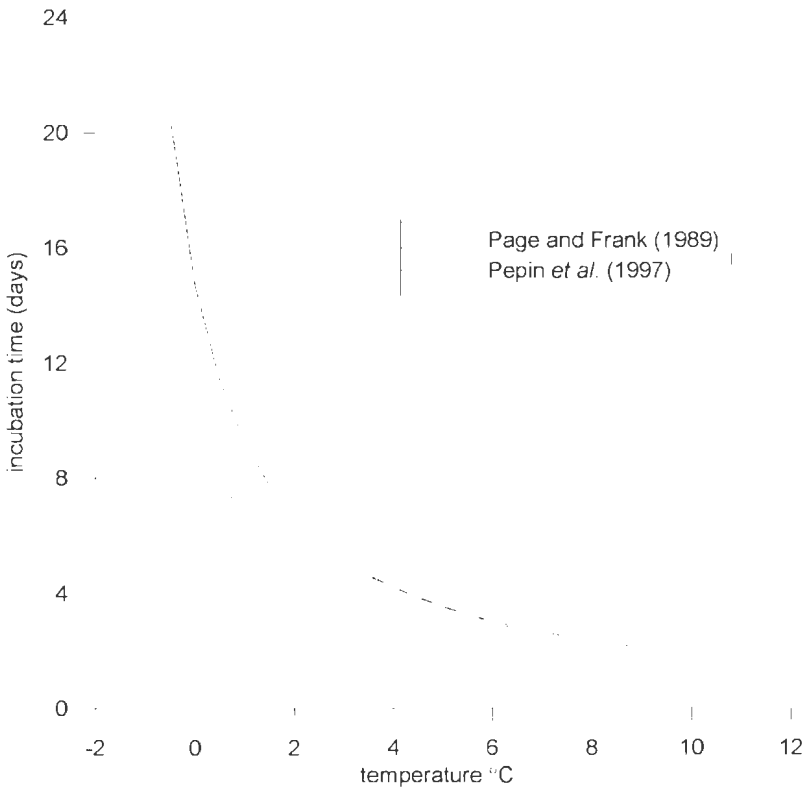

Figure 2.9 Modelled relationship between incubation time (days) and temperature (°C) for relationships from Page and Frank (1989) and Pepin *et al.* (1997).

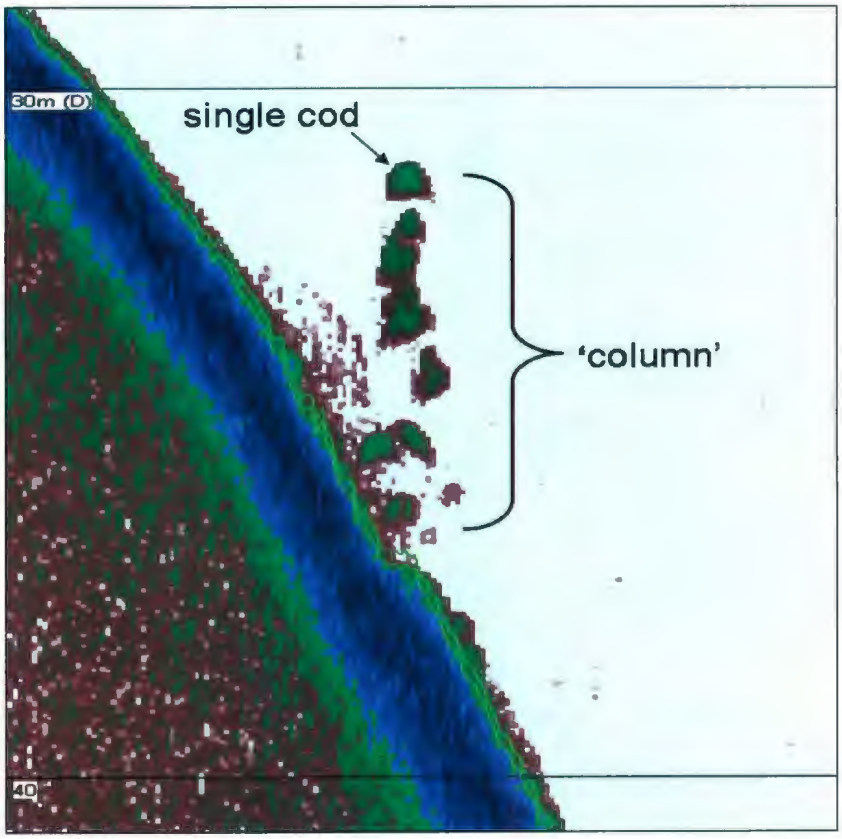

Figure 2.10 Acoustic echogram of small spawning column located near shore in Smith Sound on July 5, 2007. Horizontal lines indicate 30 and 40 m depths, echogram spans approximately 75 m, colour scales are -36dB (dark blue) to -75 (brown).

Summary

The present thesis provides evidence of multiple spawning peaks over a prolonged spawning season for Atlantic cod in a Newfoundland coastal fjord. Temporal and spatial distributions of early life stages from ichthyoplankton surveys were similar for both years of the study. Egg abundance peaked in spring, as was hypothesized, but unexpectedly, a stronger peak occurred in summer. Eggs and larvae were distributed throughout the study area in spring but became more concentrated at the inner portions of the study area in summer. Environmental data showed cooler temperatures and slower development times, higher winds with frequent changes in direction and more vertical mixing of the water column, all likely to enhance the likelihood of dispersal of eggs and larvae in spring. Conversely, warmer, calmer conditions imply faster development times and increased stratification of the water column which would enhance retention of early life stages later in the season. Overall, retention of eggs and larvae in Smith Sound appears to be substantial, but eggs and larvae may also be advected from the spawning area, especially during stormy spring weather. These findings are consistent with those on retention and advection of early life history stages in coastal areas from previous work in Newfoundland and other locations (Asplin *et al.* 1999; Bradbury *et al.* 2000; Knutsen *et al.* 2007). It is hypothesized that different peak spawning events during the season represent separate life history strategies (resident and migratory ecotypes).

Knowledge of spawning patterns and mechanisms pertaining to retention and dispersal of eggs and larvae may be useful in designing recovery strategies for collapsed cod populations in Newfoundland and other locations by allowing management to

identify and protect important spawning and nursery areas from fishing practices and other potentially detrimental anthropogenic disturbances.

In the second part of this thesis, acoustic measurements of cod behaviour were closely linked with egg production times supporting the hypothesis that vertical shoaling behaviour is associated with cod reproduction in the wild. This work demonstrates that recognizable behaviours of fishes can be used to infer biological events (e.g., spawning times). Estimated spawning times backcalculated from peaks in early stage egg abundance coincided with acoustically observed behavioural patterns (i.e., spawning columns) in both years (with the exception of late 2006 when no sampling was conducted), and indicated peak spawning activity in spring (March-April) and summer (late July). This study provides the first detailed measurements of cod spawning columns. Spatially, columns were observed extending vertically as much as 85 m in 60-235 m of water and were distributed throughout the study area in spring and near the outer portions of the Sound in summer. Fish density within columns ranged from 0.001-1.597 $kg \cdot m^2$ and showed a decrease over time. Overall, these results are consistent with previous accounts of spawning behaviour of cod (Rose 1993, Ouellet 1997, Lawson and Rose 2000a) and suggest that the release of gametes may be occurring within columns. This study confirms that columns are temporally associated with reproductive behaviour in wild cod, however, the function and composition of these structures requires further investigation.

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Appendices

Appendix 1. Number of cod eggs collected by date and development stage for study period.

	# eggs				
Sampling date	**stage 1**	**stage 2**	**stage 3**	**stage 4**	**Total**
Mar 16 2006	29	0	0	0	29
Apr 04 2006	142	8	1	0	151
Apr 06 2006	310	11	0	0	321
Apr 10 2006	221	11	0	0	232
Apr 12 2006	185	14	0	0	199
Apr 14 2006	248	22	1	0	271
Apr 18 2006	395	52	1	0	448
Apr 20 2006	358	96	6	0	460
Apr 24 2006	157	104	4	0	265
Apr 27 2006	202	177	26	0	405
May 01 2006	50	59	14	1	124
May 03 2006	56	92	51	0	199
May 10 2006	17	32	35	1	85
May 15 2006	31	37	40	12	120
May 24 2006	45	8	19	6	78
Jun 01 2006	41	12	5	0	58
Jun 06 2006	58	20	10	2	90
Jun 14 2006	96	14	2	0	112
Jun 21 2006	104	9	2	0	115
Jun 28 2006	317	17	3	0	337
Jul 06 2006	132	53	34	3	222
Jul 27 2006	594	249	58	1	902
Sep 06 2006	18	25	32	11	86
Mar 26 2007	17	1	0	0	18
Apr 03 2007	71	1	0	0	72
Apr 13 2007	92	7	0	0	99
Apr 27 2007	87	16	2	0	105
May 08 2007	21	8	3	0	32
May 16 2007	34	16	3	0	53
May 22 2007	37	8	6	0	51
May 30 2007	29	3	3	0	35
Jun 05 2007	14	1	2	0	17
Jun 13 2007	59	5	3	0	67
Jun 20 2007	35	7	7	1	50
Jun 25 2007	75	20	20	3	118
Jul 04 2007	178	42	26	1	247
Jul 11 2007	123	28	10	2	163
Jul 17 2007	355	40	17	1	413

Jul 25 2007	370	24	13	1	408
Jul 30 2007	384	52	17	1	454
Aug 06 2007	319	103	26	1	449
Aug 15 2007	186	62	39	0	287
Aug 22 2007	134	55	40	2	231
Aug 30 2007	122	69	19	1	211

Appendix 2. Maturity and size data for adult cod sampled during study period.

Date	Ship/trip no	Fish no	length (cm)	weight (kg)	sex	maturity stage
June 15 2006	CE1	1	90	6.925	f	mat ap
June 15 2006	CE1	2	83	5.404	m	spent p
June 15 2006	CE1	3	58	1.781	m	mat p
June 15 2006	CE1	4	63	2.439	m	spent p
June 15 2006	CE1	5	58	1.89	f	mat bp
June 15 2006	CE1	6	75	4.432	m	p spent
June 15 2006	CE1	7	70	3.416	m	p spent
June 15 2006	CE1	8	66	2.497	m	p spent
June 15 2006	CE1	9	72	3.71	m	p spent
June 15 2006	CE1	10	65	2.836	f	mat ap
June 15 2006	CE1	11	67	2.623	m	p spent
June 15 2006	CE1	12	55	1.368	f	imm
June 15 2006	CE1	13	81	4.646	m	p spent
June 15 2006	CE1	14	51	1.242	m	imm
June 15 2006	CE1	15	62	2.137	m	p spent
June 15 2006	CE1	16	83	5.51	m	p spent
June 15 2006	CE1	17	70	3.108	f	mat bp
June 15 2006	CE1	18	74	3.944	m	p spent
June 15 2006	CE1	19	62	2.192	m	p spent
June 15 2006	CE1	20	61	2.247	m	p spent
June 15 2006	CE1	21	58	2.083	m	p spent
June 15 2006	CE1	22	60	1.824	m	p spent
June 15 2006	CE1	23	56	1.523	m	p spent
June 15 2006	CE1	24	53	1.275	f	imm
June 15 2006	CE1	25	47	0.902	m	p spent
June 15 2006	CE1	26	43	0.725	m	imm
June 22 2006	CE2	1	62	2.291	f	mat bp
June 22 2006	CE2	2	62	2.284	f	mat bp
June 22 2006	CE2	3	59	1.614	f	imm
June 22 2006	CE2	4	70	3.48	f	mat bp
June 22 2006	CE2	5	51	1.148	m	imm
June 22 2006	CE2	6	65	2.57	f	mat ap
June 22 2006	CE2	7	75	4.296	m	p spent
June 22 2006	CE2	8	57	1.69	m	spent p
June 22 2006	CE2	9	59	1.876	f	imm
June 22 2006	CE2	10	61	2.039	f	imm
June 22 2006	CE2	11	58	1.857	m	p spent
June 22 2006	CE2	12	52	1.307	f	imm
June 22 2006	CE2	13	54	1.67	m	p spent
June 22 2006	CE2	14	51	1.193	f	imm
June 22 2006	CE2	15	67	2.878	m	p spent
June 22 2006	CE2	16	87	6.385	m	p spent

June 22 2006	CE2	17	71	3.354	m	p spent
June 22 2006	CE2	18	65	2.945	f	mat ap
June 22 2006	CE2	19	70	3.018	m	spent p
June 22 2006	CE2	20	65	2.706	m	p spent
June 22 2006	CE2	21	54	1.423	f	imm
June 22 2006	CE2	22	66	2.466	f	imm
June 22 2006	CE2	23	70	3.186	m	spent p
June 22 2006	CE2	24	67	2.471	m	p spent
June 22 2006	CE2	25	69	2.724	f	spent p
June 22 2006	CE2	26	60	2.087	f	mat ap
June 22 2006	CE2	27	71	3.302	f	spent p
June 22 2006	CE2	28	67	2.918	m	p spent
June 22 2006	CE2	29	68	2.673	m	p spent
June 22 2006	CE2	30	66	2.702	f	spent p
June 22 2006	CE2	31	76	3.886	m	p spent
June 29 2006	CE3	1	106	12.935	m	p spent
June 29 2006	CE3	2	81	5.876	m	p spent
June 29 2006	CE3	3	75	3.698	f	spent p
June 29 2006	CE3	4	69	3.29	f	mat cp
June 29 2006	CE3	5	94	7.55	m	p spent
Jan 13 2007	SH727	1	54	1.320	f	imm
Jan 13 2007	SH727	2	49	0.880	f	spent l matap
Jan 13 2007	SH727	3	51	1.080	f	imm
Jan 13 2007	SH727	4	48	0.910	f	imm
Jan 13 2007	SH727	5	55	1.360	m	spent l-mat p no milt
Jan 13 2007	SH727	6	51	1.100	m	spent l-mat p no milt
Jan 13 2007	SH727	7	50	0.920	f	imm
Jan 13 2007	SH727	8	53		m	spent l-mat p no milt
Jan 13 2007	SH727	9	75	3.710	f	spent l matap
Jan 13 2007	SH727	10	43	0.640	m	spent l-mat p no milt
Jan 13 2007	SH727	11	52		f	spent l
Jan 13 2007	SH727	12	53		f	mat ap
Jan 13 2007	SH727	13	66	2.160	m	spent l-mat p no milt
Jan 13 2007	SH727	14	44	0.790	m	imm
Jan 13 2007	SH727	15	43	0.740	f	mat ap
Jan 13 2007	SH727	16	42		m	imm
Jan 13 2007	SH727	17	47		f	imm
Jan 13 2007	SH727	18	40		m	imm
Jan 13 2007	SH727	19	37	0.460	m	imm
Jan 13 2007	SH727	20	42		m	imm
Jan 13 2007	SH727	21	34	0.320	f	imm
Jan 13 2007	SH727	22	32	0.260	m	imm
Jan 13 2007	SH727	23	24	0.100	f	imm
Jan 13 2007	SH727	24	25	0.110	f	imm
Jan 13 2007	SH727	25	22	0.070	m	imm
Jan 13 2007	SH727	26	19	0.050	m	imm

Jan 13 2007	SH727	27	18	0.040	f	imm
Jan 13 2007	SH727	28	17	0.030	m	imm
Jan 13 2007	SH727	29	18	0.040	f	imm
Jan 13 2007	SH727	30	18	0.040	m	imm
Jan 13 2007	SH727	31	15		f	imm
Jan 13 2007	SH727	32	17		m	imm
Jan 13 2007	SH727	33	17		m	imm
Jan 13 2007	SH727	34	17		f	imm
Jan 13 2007	SH727	35	98	9.340	f	spent I matap
Jan 13 2007	SH727	36	89	6.520	f	spent I matap
Jan 13 2007	SH727	37	83	5.710	m	spent I -matp
Jan 13 2007	SH727	38	54		m	spent I-mat p no milt
Jan 13 2007	SH727	39	59		m	spent I -matp
Jan 13 2007	SH727	40	62	2.220	m	spent I-mat p no milt
Jan 13 2007	SH727	41	82	5.410	f	spent I matap
Jan 13 2007	SH727	42	52		f	imm
Jan 13 2007	SH727	43	77	4.270	f	spent I matap
Jan 13 2007	SH727	44	100	10.110	m	spent I-mat p no milt
Jan 13 2007	SH727	45	96	8.980	f	spent I matap
Jan 13 2007	SH727	46	86		f	spent I matap
Jan 13 2007	SH727	47	85	5.910	m	spent I
Jan 13 2007	SH727	48	90	5.860	f	spent I matap
Jan 13 2007	SH727	49	83	4.860	f	spent I matap
Jan 13 2007	SH727	50	56		m	spent I -matp
Jan 13 2007	SH727	51	68	3.120	m	spent I-mat p no milt
Jan 13 2007	SH727	52	58		f	mat ap
Jan 13 2007	SH727	53	86		m	spent I-mat p no milt
Jan 13 2007	SH727	54	51		f	imm
Jan 13 2007	SH727	55	58		f	imm
Jan 13 2007	SH727	56	50		f	imm
Jan 13 2007	SH727	57	49		f	spent I matap
Jan 13 2007	SH727	58	72	2.870	m	spent I-mat p no milt
Jan 13 2007	SH727	59	55		f	imm
Jan 13 2007	SH727	60	49		f	imm
Jan 13 2007	SH727	61	50		f	imm
Jan 13 2007	SH727	62	49		m	spent I-mat p no milt
Jan 13 2007	SH727	63	52		f	imm
Jan 13 2007	SH727	64	52		f	imm
Jan 13 2007	SH727	65	54		f	imm
Jan 13 2007	SH727	66	43		f	imm
Jan 13 2007	SH727	67	52		f	imm
Jan 13 2007	SH727	68	48		m	spent I-mat p no milt
Jan 13 2007	SH727	69	45		m	spent I-mat p no milt
Jan 13 2007	SH727	70	37	0.420	m	imm
Jan 13 2007	SH727	71	25	0.140	f	imm
Jan 13 2007	SH727	72	19		m	imm

Jan 13 2007	SH727	73	18		f	imm
Jan 13 2007	SH727	1	52	1.140	f	imm
Jan 13 2007	SH727	2	57	1.420	m	spent l-mat p no milt
Jan 13 2007	SH727	3	48	0.900	m	spent l-mat p no milt
Jan 13 2007	SH727	4	51	1.040	m	spent l-mat p no milt
Jan 13 2007	SH727	5	47	0.900	f	imm
Jan 13 2007	SH727	6	46	0.760	f	imm
Jan 13 2007	SH727	7	39	0.560	m	imm
Jan 13 2007	SH727	8	40	0.530	f	imm
Jan 13 2007	SH727	9	44	0.700	f	imm
Jan 13 2007	SH727	10	39	0.500	m	imm
Jan 13 2007	SH727	11	39	0.460	f	imm
Jan 13 2007	SH727	12	31	0.240	m	imm
Jan 13 2007	SH727	13	29	0.190	f	imm
Jan 13 2007	SH727	14	27	0.140	m	imm
Jan 13 2007	SH727	15	33	0.280	f	imm
Jan 13 2007	SH727	16	24	0.100	f	imm
Jan 13 2007	SH727	17	23	0.090	m	imm
Jan 13 2007	SH727	18	19	0.050	m	imm
Jan 13 2007	SH727	19	17	0.030	m	imm
Jan 13 2007	SH727	20	19	0.050	m	imm
Jan 13 2007	SH727	21	17	0.040	m	imm
Jan 13 2007	SH727	22	18	0.040	f	imm
Jan 13 2007	SH727	23	15		m	imm
Jan 13 2007	SH727	24	17		f	imm
Jan 13 2007	SH727	25	22	0.080	f	imm
Jan 13 2007	SH727	26	19		m	imm
Jan 13 2007	SH727	27	20		f	imm
Jan 13 2007	SH727	28	18		f	imm
Jan 13 2007	SH727	29	16		f	imm
Jan 13 2007	SH727	30	19		m	imm
Jan 13 2007	SH727	31	20		f	imm
Jan 13 2007	SH727	32	19		m	imm
Jan 13 2007	SH727	33	15		m	imm
Jan 13 2007	SH727	34	15		m	imm
Jan 13 2007	SH727	35	0		f	imm
Jan 13 2007	SH727	36	15		m	imm
Jan 13 2007	SH727	37	18		m	imm
Jan 13 2007	SH727	38	15		m	imm
Jan 13 2007	SH727	39	12		m	imm
Jan 13 2007	SH727	40	18		m	imm
Jan 13 2007	SH727	41	20		f	imm
Jan 13 2007	SH727	42	17		f	imm
Jan 13 2007	SH727	43	18		m	imm
Jan 13 2007	SH727	44	20		f	imm
Jan 13 2007	SH727	45	14		m	imm

Jan 13 2007	SH727	46	18		m	imm
Jan 13 2007	SH727	47	16		m	imm
Jan 13 2007	SH727	48	19		f	imm
Jan 13 2007	SH727	49	19		m	imm
Jan 13 2007	SH727	50	18		f	imm
Jan 13 2007	SH727	51	16		m	imm
Jan 13 2007	SH727	52	16		m	imm
Jan 13 2007	SH727	53	16		m	imm
Jan 13 2007	SH727	54	15		m	imm
Jan 13 2007	SH727	1	103		f	spent l matap
Jan 13 2007	SH727	2	70	3.040	f	spent l matap
Jan 13 2007	SH727	3	65	2.450	f	spent l matap
Jan 13 2007	SH727	4	61	1.620	m	spent l
Jan 13 2007	SH727	5	76	4.630	f	spent l matap
Jan 13 2007	SH727	6	60	1.880	f	spent l matap
Jan 13 2007	SH727	7	56	1.550	m	spent l-mat p no milt
Jan 13 2007	SH727	8	52	1.040	m	spent l-mat p no milt
Jan 13 2007	SH727	9	56	1.540	f	spent l matap
Jan 13 2007	SH727	10	55	1.460	f	spent l
Jan 13 2007	SH727	11	53	1.200	m	spent l-mat p no milt
Jan 13 2007	SH727	12	50		m	spent l-mat p no milt
Jan 13 2007	SH727	13	53		m	spent l-mat p no milt
Jan 13 2007	SH727	14	51		f	imm
Jan 13 2007	SH727	15	55		f	imm
Jan 13 2007	SH727	16	49	1.000	f	imm
Jan 13 2007	SH727	17	48	0.770	f	imm
Jan 13 2007	SH727	18	49	0.800	m	spent l-mat p no milt
Jan 13 2007	SH727	19	46	0.780	f	imm
Jan 13 2007	SH727	20	43	0.640	f	imm
Jan 13 2007	SH727	21	14	0.020	m	imm
Jan 13 2007	SH727	22	18	0.040	m	imm
Jan 13 2007	SH727	23	12	0.010	m	imm
Jan 15 2006	SH653	1	54	1.290	m	spent l -matp
Jan 15 2006	SH653	2	67	2.470	f	spent l
Jan 15 2006	SH653	3	58	1.410	m	spent l -matp
Jan 15 2006	SH653	4	66	2.395	f	spent l
Jan 15 2006	SH653	5	43	0.565	f	imm
Jan 15 2006	SH653	6	62	1.860	m	matp
Jan 15 2006	SH653	7	62	1.770	f	matap
Jan 15 2006	SH653	8	71	3.380	m	matp
Jan 15 2006	SH653	9	52	1.195	f	matan
Jan 15 2006	SH653	10	46	0.800	m	spent l
Jan 15 2006	SH653	11	45	0.780	m	spent l -matp with milt
Jan 15 2006	SH653	12	56	1.405	f	spent l matap
Jan 15 2006	SH653	13	64	2.030	f	spent l matap
Jan 15 2006	SH653	14	65	2.615	f	spent l matap

Jan 15 2006	SH653	15	54	1.345	m	mat p
Jan 15 2006	SH653	16	44	0.655	f	imm
Jan 15 2006	SH653	17	72	3.410	m	matp
Jan 15 2006	SH653	18	76	3.730	m	spent l-matp with milt
Jan 15 2006	SH653	19	62	1.945	f	spent l
Jan 15 2006	SH653	20	64	2.460	m	spent l-matp with milt
Jan 15 2006	SH653	21	66	2.800	f	spent l matap
Jan 15 2006	SH653	22	57	1.510	f	matap
Jan 15 2006	SH653	23	45	0.685	f	imm
Jan 15 2006	SH653	24	47	0.875	m	spent l-matp with milt
Jan 15 2006	SH653	25	49	0.935	f	matap
Jan 15 2006	SH653	26	46	0.840	m	spent l-matp with no milt
Jan 15 2006	SH653	27	71	3.070	f	spent l matap
Jan 15 2006	SH653	28	54	1.505	f	spent l matap
Jan 15 2006	SH653	29	57	1.705	f	spent l matap
Jan 15 2006	SH653	30	40	0.615	m	imm
Jan 15 2006	SH653	31	43	0.635	f	imm
Jan 15 2006	SH653	32	42	0.775	f	imm
Jan 15 2006	SH653	33	39	0.465	f	imm
Jan 15 2006	SH653	34	69	3.125	f	matap
Jan 15 2006	SH653	35	58	1.665	m	spent l-mat p with milt
Jan 15 2006	SH653	36	63	1.845	m	spent l-matp no milt
Jan 15 2006	SH653	37	59	1.885	m	spent l -matp with milt
Jan 15 2006	SH653	38	58	1.800	m	spent l-matp with milt
Jan 15 2006	SH653	39	40	0.675	f	imm
Jan 15 2006	SH653	40	41	0.645	m	imm
Jan 15 2006	SH653	41	46	0.800	f	imm
Jan 15 2006	SH653	42	66	2.250	f	spent l-mat ap
Jan 15 2006	SH653	43	44	0.760	m	spent l-matp with no milt
Jan 15 2006	SH653	44	57	1.370	f	spent l
Jan 15 2006	SH653	45	38	0.465	f	imm
Jan 15 2006	SH653	46	35	1.390	m	imm
Jan 15 2006	SH653	47	56	1.400	f	spent l mat ap
Jan 15 2006	SH653	48	50	1.070	m	spent l-mat p with milt
Jan 15 2006	SH653	49	53	1.330	m	spent l-mat p with milt
Jan 15 2006	SH653	50	54	1.415	f	spent l
Jan 15 2006	SH653	51	39	0.530	m	imm
Jan 15 2006	SH653	52	44	0.690	f	imm
Jan 15 2006	SH653	53	49	1.005	m	spent l-mat p with no milt
Jan 15 2006	SH653	60	33	0.295	f	imm
Jan 15 2006	SH653	61	63	2.305	m	mat p
Jan 15 2006	SH653	62	69	2.655	f	spent l
Jan 15 2006	SH653	64	60	1.800	m	spent l-matp with milt
Jan 15 2006	SH653	65	52	1.275	f	spent l mat ap
Jan 15 2006	SH653	66	42	0.635	f	imm
Jan 15 2006	SH653	68	38	0.430	f	imm

Jan 15 2006	SH653	70	37	0.485	f	imm
Jan 15 2006	SH653	1	82	5.300	f	mat ap
Jan 15 2006	SH653	2	76	3.775	f	mat ap
Jan 15 2006	SH653	3	59	1.635	f	spent I
Jan 15 2006	SH653	4	67	3.020	f	mat ap
Jan 15 2006	SH653	5	59	5.835		
Jan 15 2006	SH653	6	57	1.730	m	spent I-mat p with milt
Jan 15 2006	SH653	7	70	3.360	f	spent I
Jan 15 2006	SH653	8	62	2.220	m	spent I-mat p with milt
Jan 15 2006	SH653	9	67	2.245	f	spent I
Jan 15 2006	SH653	10	55	1.355	f	spent I
Jan 15 2006	SH653	11	72	3.805	m	spent I-matp with milt
Jan 15 2006	SH653	12	63	2.245	f	spent I
Jan 15 2006	SH653	13	76	3.855	f	mat ap
Jan 15 2006	SH653	14	94	6.920	f	spent I-mat ap
Jan 15 2006	SH653	15	65	2.290	f	spent I
Jan 15 2006	SH653	16	82	5.745	m	spent I-mat p with milt
Jan 15 2006	SH653	17	82	5.325	m	spent I-mat p with milt
Jan 15 2006	SH653	18	68	2.805	f	spent I
Jan 15 2006	SH653	19	65	2.595	m	spent I-mat p with milt
Jan 15 2006	SH653	20	67	2.615	m	spent I-mat p no milt
Jan 15 2006	SH653	21	54	1.170	f	spent I
Jan 15 2006	SH653	22	78	4.435	f	spent I mat ap
Jan 15 2006	SH653	23	78	4.845	m	spent I-mat p with milt
Jan 15 2006	SH653	24	62	1.995	f	spent I
Jan 15 2006	SH653	25	79	5.010	f	mat ap
Jan 15 2006	SH653	26	72	3.680	f	
Jan 15 2006	SH653	27	79	3.980	f	mat ap
Jan 15 2006	SH653	28	62	2.285	m	spent I-mat p with milt
Jan 15 2006	SH653	29	70	3.475	m	spent I-mat p with milt
Jan 15 2006	SH653	30	68	3.035	m	spent I-mat p with milt
Jan 15 2006	SH653	31	72	3.325	f	spent I mat ap
Jan 15 2006	SH653	32	79	4.025	f	spent I-mat ap
Jan 15 2006	SH653	33	64	2.225	f	spent I
Jan 15 2006	SH653	34	76	4.410	m	spent I-mat p with milt
Jan 15 2006	SH653	35	87	6.855	f	mat ap
Jan 15 2006	SH653	36	56	1.490	m	spent I-mat p with milt
Jan 15 2006	SH653	37	86	3.175	m	spent I-mat p with milt
Jan 15 2006	SH653	38	71	3.270	f	spent I mat ap
Jan 15 2006	SH653	40	71	3.125	f	spent I
Jan 15 2006	SH653	41	81	4.255	f	spent I
Jan 15 2006	SH653	42	94	9.445	f	spent I mat ap
Jan 15 2006	SH653	43	98	9.895	f	spent I
Jan 15 2006	SH653	44	63	2.440	f	mat ap
Jan 15 2006	SH653	45	60	1.825	f	spent I
Jan 15 2006	SH653	47	75	4.725	f	spent I

Jan 15 2006	SH653	48	83	5.075	m	spent l-mat p with milt
Jan 15 2006	SH653	49	68	2.855	m	spent l-mat p with milt
Jan 15 2006	SH653	50	78	4.635	m	spent l-mat p with milt
Jan 15 2006	SH653	51	83	6.305	m	mat p
Jan 15 2006	SH653	52	66	2.630	f	spent l
Jan 15 2006	SH653	53	70	3.245	f	mat ap
Jan 15 2006	SH653	54	80	4.455	f	spent l mat ap
Jan 15 2006	SH653	55	80	4.350	f	spent l
Jan 15 2006	SH653	56	54	1.245	m	spent l-mat p no milt
Jan 15 2006	SH653	60	77	4.625	m	mat p
Jan 15 2006	SH653	61	64	2.755	m	spent l-mat p with milt
Jan 15 2006	SH653	63	117	16.865	f	spent l mat ap
Jan 15 2006	SH653	64	58	1.810	f	mat ap
Jan 15 2006	SH653	65	61	2.195	f	spent l
Jan 15 2006	SH653	66	84	6.285	m	spent l-mat p with milt
Jan 15 2006	SH653	74	74	3.920	m	spent l-mat p with milt
Jan 15 2006	SH653	77	73	3.600	m	spent l-mat p with milt
Jan 15 2006	SH653	83	69	2.925	f	mat ap
Jan 15 2006	SH653	89	92	8.095	m	spent l-mat p with milt
Jan 15 2006	SH653	90	53	1.440	m	spent l-mat p with milt
Jan 15 2006	SH653	116	122		f	spent l mat ap
May 7 2007	SH780	1	89	7.24	f	mat a
May 7 2007	SH780	2	98	10	f	mat b
May 7 2007	SH780	3	74	3.58	m	spent p
May 7 2007	SH780	4	87	6.1	f	mat a
May 7 2007	SH780	5	106	11.1	f	mat a
May 7 2007	SH780	6	96	7.9	f	mat a
May 7 2007	SH780	7	91	6	m	mat p
May 7 2007	SH780	8	94	7.1	m	mat p
May 7 2007	SH780	9	73	3.2	f	mat a
May 7 2007	SH780	10	95	7.7	f	mat a
May 7 2007	SH780	11	91	7.56	f	mat a
May 7 2007	SH780	12	92	7.9	m	mat p
May 7 2007	SH780	13	74	3.25	m	mat p
May 7 2007	SH780	14	98	9.7	m	mat p
May 7 2007	SH780	15	88	6.4	f	mat b
May 7 2007	SH780	16	83	5.1	m	mat p
May 7 2007	SH780	17	106	>12	f	mat c
May 7 2007	SH780	18	91	7	f	mat a
May 7 2007	SH780	19	99	9.8	f	mat a
May 7 2007	SH780	20	98	9.9	f	mat b
May 7 2007	SH780	21	69	2.9	m	mat p
May 7 2007	SH780	22	84	6.36	f	mat c
May 7 2007	SH780	23	91	5.9	m	mat p
May 7 2007	SH780	24	100	8.8	f	mat a
May 7 2007	SH780	25	90	7.4	f	mat a

May 7 2007	SH780	26	88	6.8	m	mat p
May 7 2007	SH780	27	101	9.8	f	mat a
May 7 2007	SH780	28	99	9.8	f	mat b
May 7 2007	SH780	29	101	9.6	f	mat b
May 7 2007	SH780	30	86	5.2	f	mat a
May 7 2007	SH780	31	91	7.2	m	mat p
May 7 2007	SH780	32	90	6.5	m	mat p
May 7 2007	SH780	33	95	7.1	m	mat p
May 7 2007	SH780	34	93	8.3	m	mat p
May 7 2007	SH780	35	86	5	m	mat p
May 7 2007	SH780	36	88	6.86	f	mat a
May 7 2007	SH780	37	53	1.2	m	imm
May 7 2007	SH780	38	94	7.8	m	mat p
May 7 2007	SH780	39	71	2.8	m	mat p
May 7 2007	SH780	40	75	3.7	f	mat a
May 7 2007	SH780	41	69	3	m	mat p
May 7 2007	SH780	42	89	6.7	f	mat a
May 7 2007	SH780	43	84	6	f	mat a